# PROCEEDINGS

OF THE

GENERAL MEETINGS FOR SCIENTIFIC BUSINESS

OF THE

# ZOOLOGICAL SOCIETY

# OF LONDON.

1926, pp. 683–1314,

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1926–1927.

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(1926, pp. 683–1314.)

# ZOOLOGICAL SOCIETY OF

## INSTRUCTIONS TO AUTHORS.

Owing to the cost of printing, the Publication Committee beg to draw the attention of Authors submitting papers for publication by the Society to the following Regulations. If the conditions are not observed, papers may have to be returned: —

1. MSS. submitted for publication must be written in a clear and legible handwriting, or, preferably, be type-written, and must be in final form for printing. The MSS. should be written on one side of each sheet only, and the pages clearly numbered. All tables of contents, references to plates, or legends to illustrations in the text, etc., must be in their proper places, **with page and plate numbers left blank**; and the position for the text figures must be indicated. References to literature must be exact, with the page number as well as the volume number and date.

2. Proofs and their Correction.—Two copies of the slip proof, and a page proof for final revision, will be sent to the Author, **but it is important that all serious corrections be made on the slip proof.** Expenses for proof corrections are very heavy, but, if the MSS. comply with Regulation 1, should not exceed 25 per cent of the printers' charges. If the cost of corrections exceeds 25 per cent., a proportion of the excess will be charged to the Author.

3. Revised proofs must, if possible, be returned within one week from the date of their receipt by the Author.

4. The Author receives 30 copies of reprints free, and, with the sanction of the Publication Committee, may obtain leave to buy extra copies, at the cost price charged by the printers and engravers to the Society. The number of separate copies required must be stated when returning the proof.

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*Note.*—The Publication Committee is always ready to give Authors who apply for it, permission to reproduce matter that they have contributed to the Society's "Proceedings" and "Transactions," but the Society has been advised that a formal assignment from Authors is necessary to enable it to protect copyright against third parties.

# ZOOLOGICAL SOCIETY OF LONDON.

This Society was founded in 1826 by Sir Stamford Raffles, Mr. J. Sabine, Mr. N. A. Vigors, and other eminent Naturalists, for the advancement of Zoology and Animal Physiology, and for the introduction of new and curious subjects of the Animal Kingdom, and was incorporated by Royal Charter in 1829.

**Patron.**

HIS MAJESTY THE KING.

## COUNCIL.

The Society consists of Fellows, Imperial Fellows, Honorary, Foreign, and Corresponding Members, elected according to the By-Laws. It carries out the objects of its foundation by means of its collection of living animals, by its Library, and by its Scientific Publications.

The Office of the Society, Regent's Park, N.W.8, where all communications should be sent, addressed to "The Secretary," is open from Ten till Five, except on Saturdays, when it closes at ONE P.M.

The Library, under the superintendence of Mr. F. Martin Duncan, F.R.M.S., F.R.P.S., F.Z.S., is open daily (except Sunday) from Ten A.M. till Five P.M.; on Saturdays, Ten A.M. till One P.M.

The Library is closed from Good Friday to Easter Monday, and upon all other Bank Holidays. It is also closed annually for cleaning during the month of September.

The Meetings of the Society for General Business are held in the Meeting Room at the Society's Office on the third Wednesday of the month at 4.30 P.M. except in September and October.

The Meetings for Scientific Business are held in the Meeting Room at the Society's Office fortnightly on Tuesdays, except in July, August, September, and December and January, at half-past Five o'clock P.M.

The Anniversary Meeting is held on the 29th of April, or the nearest convenient day, at Four P.M.

The Society's Gardens are open daily from Nine o'clock until Sunset, or 8 P.M. when sunset is later. Dr. G. M. Vevers is the Superintendent, Mr. D. Seth-Smith, Curator of Mammals and Birds; Mr. Edward G. Boulenger is Director of the Aquarium; Miss Joan B. Procter, F.L.S., is Curator of Reptiles; Mr. L. C. Bushby, F.E.S., is Curator of Insects; Dr. John Beattie, M.B., Ch.B., M.Sc., is Anatomist; Dr. H. H. Scott, M.D., F.R.C.P., D.P.H., Pathologist; Prof. R. T. Leiper, F.R.S., with the assistance of a panel of experts, examines and reports on the Parasites; Prof. G. H. Wooldridge, F.R.C.V.S., is Honorary Consulting Veterinary Surgeon; and Dr. R. W. A. Salmond, O.B.E., Honorary Radiologist to the Society. Applications for anatomical or pathological material, or for facilities for work in the Prosectorium should be addressed to the Secretary.

## TERMS FOR THE ADMISSION OF FELLOWS.

FELLOWS pay an Admission Fee of £5, and an Annual Contribution of £3, due on the 1st of January, and payable in advance, or a Composition of £45 in lieu thereof; the whole payment, including the Admission Fee, being £50.

No person can be deemed a FELLOW until the Admission Fee and first Annual Subscription of £3 have been paid, or the annual payments have been compounded for.

The usual Admission Fee of £5 is waived upon the election of the WIFE or HUSBAND of an existing FELLOW.

**The First Annual Subscription of Fellows elected in November and December covers the following year.**

# PRIVILEGES OF FELLOWS.

FELLOWS have Personal Admission to the Gardens upon signing their names in the book at the entrance gate, and may introduce Two Companions daily.

The WIFE or HUSBAND of a FELLOW can exercise these privileges in the absence of the Fellow, but this privilege cannot be extended to children of Fellows.

Until further notice, FELLOWS will receive 40 undated Green Cards, available on any Sunday or week-day up to the end of February of the year following the year of issue, and 20 White Cards available on any week-day up to the same date. Special children's tickets are no longer issued, but the Green and White Cards are perforated, and each half is valid for a Child under twelve years of age. It is particularly requested that Fellows *will sign every ticket* before it goes out of their possession. Unsigned tickets are not valid.

FELLOWS are not allowed to pass in friends on their written order or on presentation of their visiting cards.

AQUARIUM.—From January 1st. 1925, until further notice, FELLOWS have free personal admission to the Aquarium at all times when it is open. On Sundays, but not on week-days, they may introduce two visitors with them. These privileges are personal and cannot be transferred. For admission to the Aquarium of other friends whom they have admitted to the Gardens by Sunday tickets they may purchase from the Office books of 20 tickets for £1, or a smaller number at the same rate, each ticket admitting one adult or two children on Sundays or week-days. FELLOWS may also purchase a transferable AQUARIUM IVORY TICKET, for £10, valid for the whole duration of the Fellowship and admitting daily, on Sundays or week-days, two persons who have already gained admission to the Gardens.

FELLOWS have the privilege of receiving the Society's ordinary Publications issued during the year upon payment of the additional Subscription of One Guinea. This Subscription is due upon the 1st of January, and must be paid before the day of the Anniversary Meeting, after which the privilege lapses. FELLOWS are likewise entitled to purchase these Publications at 20 per cent. less than the price charged to the public. A further reduction of 20 per cent. is also made upon all purchases of Publications issued prior to 1881, if above the value of Five Pounds.

FELLOWS also have the privilege of subscribing to the Annual Volume of 'The Zoological Record,' which gives a list of the Works and Publications relating to Zoology in each year, for the sum of Two Pounds Ten Shillings. Separate divisions of volumes 39 onwards can also be supplied. Full particulars of these publications can be had on application to the Secretary.

Fellows may obtain a Transferable Ivory Ticket admitting two persons, available throughout the whole period of Fellowship, on payment of Ten Pounds in one sum. A second similar ticket may be obtained on payment of a further sum of Twenty Pounds.

Any Fellow who intends to be absent from the United Kingdom during the space of at least one year, may, upon giving to the Secretary notice in *writing*, have his or her name placed upon the "dormant list," and will then be called upon to pay an annual subscription of £1 only during such absence, or in the event of returning to the United Kingdom before June 30th in any year to pay the balance of the ordinary subscription. After three years a Dormant Fellow must make a further application to be retained on that list.

Any Fellow, having paid all fees due to the Society, is at liberty to withdraw his or her name upon giving notice in *writing* to the Secretary.

Ladies or Gentlemen wishing to become Fellows of the Society are requested to communicate with "The Secretary."

P. CHALMERS MITCHELL,
*Secretary.*

Regent's Park, London, N.W. 8.
December, 1926.

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## *MEETINGS*

OF THE

# ZOOLOGICAL SOCIETY OF LONDON

FOR

## SCIENTIFIC BUSINESS.

**1927.**

| | | | |
|---|---|---|---|
| Tuesday, | February ......... | 8 and 22. | |
| ——— | March ........... | 8 ,, 22. | |
| ——— | April............. | 5 ,, 26. | |
| ——— | May .............. | 10 ,, 24. | |
| ——— | June .. ........... | 7 — | |

***The Chair will be taken at half-past Five o'clock precisely.***

# ZOOLOGICAL SOCIETY OF LONDON.

## LIST OF PUBLICATIONS.

THE scientific publications of the Zoological Society of London are of two kinds—"Proceedings," published in an octavo form, and "Transactions," in quarto.

According to the present arrangements, the "Proceedings" contain not only notices of all business transacted at the scientific meetings, but also all the papers read at such meetings and recommended to be published in the "Proceedings" by the Committee of Publication. A large number of coloured plates and engravings are issued in the volumes of the "Proceedings," to illustrate the new or otherwise remarkable species of animals described therein. Amongst such illustrations, figures of the new or rare species acquired in a living state for the Society's Gardens are often given.

The "Proceedings" for each year are issued in four parts, paged consecutively, during the months of March, June, September, and December. From January 1901 they have been issued as two half-yearly volumes, indexed separately.

An "Abstract of the Proceedings" is published by the Society on the Tuesday following the date of the Scientific Meeting to which it refers. It is issued along with the "Proceedings," free of extra charge, to all Fellows who subscribe to the Publications, but it may be obtained on the day of publication at the price of Sixpence, or, if desired, sent post free for the sum of Six Shillings per annum, payable in advance.

The "Transactions" contain such of the communications made to the Scientific Meetings of the Society as, on account of the nature of the plates required to illustrate them, are better adapted for publication in the quarto form. They are issued at irregular intervals.

Fellows and Corresponding Members, upon payment of a Subscription of One Guinea *before* the day of the Anniversary Meeting, are entitled to receive the Society's Publications for the year. They are likewise entitled to purchase the Publications of the Society at 20 per cent. less than the price charged to the Public. A further reduction of 20 per cent. is made upon purchases of Publications issued prior to 1881, if they exceed the value of Five Pounds.

Fellows also have the privilege of subscribing to the Zoological Record for a sum of Two Pounds Ten Shillings (which includes cost of delivery), payable on the 1st of July in each year; but this privilege is forfeited unless the subscription be paid *before* the 1st of December following.

The following is a complete list of the publications of the Society already issued.

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| „ XXI.—Part I. (7 Plates & 12 Text-figs.) | | (June 1916) | 2 5 0 | 3 0 0 |
| „ XXII.—Part I. (Text-figures 1–13) | | (December 1926) | 1 17 6 | 2 10 0 |

In consequence of a re-arrangement of the stock of the 'Transactions,' the Society is now able to offer for sale, at the reduced price of £30, sets of Vols. V.–XVI. inclusive.

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* 1908 out of print. † 1911 out of print.

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**ZOOLOGICAL RECORD.**—Vol. 61, containing literature relating chiefly to the year 1924, has now been published, price £3. Vol. 62, for the year 1925, is being prepared as usual, price £3, or subscription, if paid in advance, £2 10*s*. 0*d*.

P. CHALMERS MITCHELL,
*Secretary*.

Regent's Park, London, N.W. 8.
December 1926.

*These publications may be obtained at the* SOCIETY'S OFFICE *or through any bookseller.*

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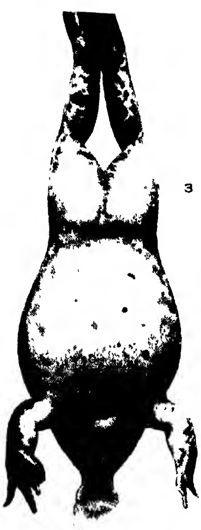

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A MYCOTIC DISEASE OF BATRACHIANS.

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A MYCOTIC DISEASE OF BATRACHIANS.

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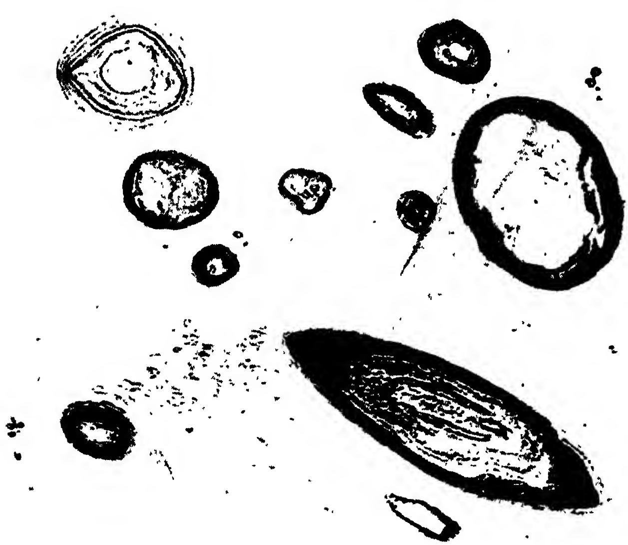

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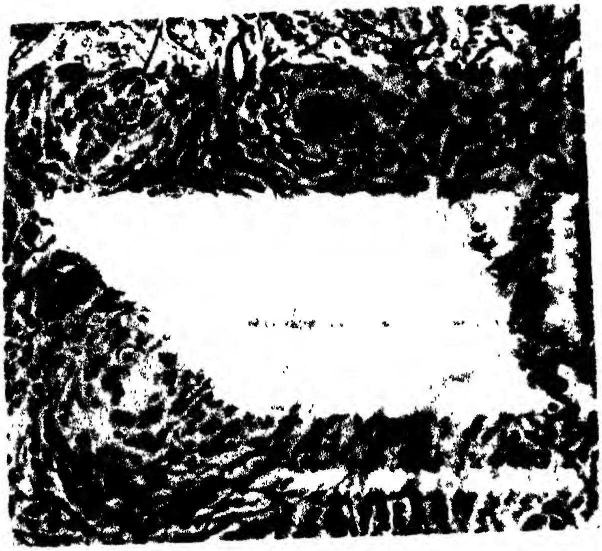

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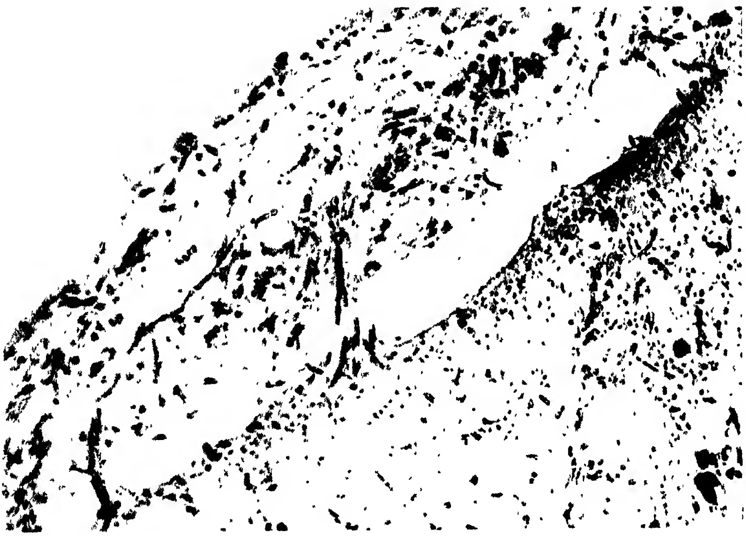

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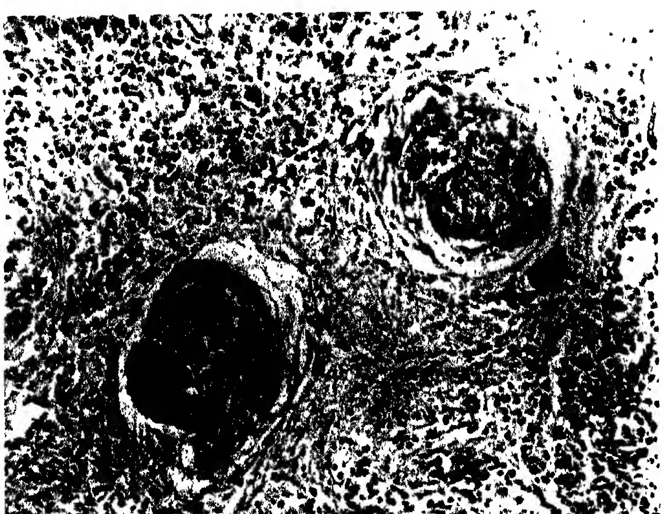

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# PROCEEDINGS

OF THE

# GENERAL MEETINGS FOR SCIENTIFIC BUSINESS

# ZOOLOGICAL SOCIETY OF LONDON.

## PAPERS.

## 31. A Mycotic Disease of Batrachians. By H. HAROLD SCOTT, M.D., F.R.C.P.Lond., D.P.H., D.T.M.H.Camb., F.R.S. Edin., F.Z.S., Pathologist to the Society.

[Received March 29, 1926: Read June 15, 1926.]

(Plates I–V.*)

The disease whose clinical history and pathology is the subject of this paper is one which has been responsible for a considerable mortality amongst Batrachians during 1925.

I am not in a position to say whether it has been equally prevalent, or equally fatal, in other years, because I can find but little record of the condition, and no detailed work appears to have been undertaken in respect of it.

Previous records on the prevalence of this condition or anything which can be so interpreted are very meagre. I have searched the 'Proceedings of the Zoological Society' for the last fifteen years. Cases are now and then recorded of reptiles dying from mycosis, but, as a rule, no particular notice is taken of it, the mammalian, avian, and reptilian all being placed under the same heading. There is one instance recorded as occurring in 1909 in which the fungus is stated to have been *Aspergillus fumigatus*; this must have been a different condition from that dealt with in the present paper. There are only two statements which appear to refer definitely to this. In the Report on the Deaths occurring in 1914 (P. Z. S. 1915, p. 127) mycosis is given as the cause of

* For explanation of the Plates, see p. 692.

death in ten reptiles, and Dr. Plimmer states: "It . . . . has been found in the larger frogs and tortoises. It is produced in them by a much larger mould than that found in the mammals and birds, which generally leads to the formation of tumours." Again, in the following year (P. Z. S. 1916, p. 82), "A Ceratodus, which had been many years in the Gardens, died from a mould disease of the skin, similar to that from which several of the larger toads and frogs have died."

Lastly, there is a specimen preserved from a Bull-Frog in 1921 in which the liver appeared to resemble in all points that found in similar animals dying during 1925. The cause of death was recorded as cirrhosis of liver. I removed a fragment of this, cut and stained it, and found the condition such as will be described later under pathological histology.

I have been able to obtain very little evidence relative to the existence of this condition elsewhere; in fact, scientifically speaking, there is no trustworthy evidence. I have been given to understand that there is a disease which kills a large number of toads and frogs kept in laboratories or in the shops of dealers who maintain a considerable stock. The signs, so far as they have been noted (in most instances no special attention has been paid to this point), have resembled what has been seen here, but the high mortality has been ascribed to overcrowding and not to any specific disease. If the condition is the same as the one about to be described, overcrowding and close contact would certainly play a part in assisting its dissemination.

Since the beginning of the year several Salamanders died of the disease, 5 Bull-Frogs (*Rana catesbiana*), 5 Black-spotted Toads (*Bufo melanostictus*), 8 Square-marked Toads (*Bufo regularis*), 1 American Toad, and 1 White's Tree-Frog. Others have been attacked by it, but died from some intercurrent disease, or were accorded euthanasia when the condition became severe and proved refractory to all treatment, while a few, coming under observation in an early stage, were treated and recovered. Among these were an African Toad, an Indian Toad, and a Common Frog. It is not possible, therefore, to state definitely the mortality from this affection, since in some its lesions merely served as a predisposing cause to other diseases. In twenty at least death was clearly ascribable to it.

The ensuing account of the semeiology of this disease is based upon information very kindly given to me by the Curator of Reptiles, Miss Joan Procter*.

The course of the disease differs somewhat according to the animal attacked. In Salamanders it is, I understand, met with fairly frequently, and is known in the trade as "Salamander disease." In this animal it usually starts at the tip of the nose as a small erosion, probably preceded by a slight swelling which

* I am desirous of expressing my indebtedness to Miss Procter, not only for this information, but also for her kindness in affording me facilities for seeing cases during life and examining the condition in the earlier stages.

soon breaks down to form a shallow ulcer. In the discharge from this ulcer, and also in the secretion from its undermined edges, hyphæ of a mould are seen, sometimes single, more often as a feltwork of several. After a variable period, usually short, the ulcer extends both in area and in depth, spreads to the bone, and, finally, when death occurs, the whole of the front of the face has been eroded and eaten away. Sometimes ulcers are to be seen on the limbs. It is possible, of course, that there is first a small sore, an abrasion, produced by some trivial injury, and on this the mould finds a ready site for growth when once it becomes implanted.

In Frogs and Toads the primary lesion may be on the nose, but is nearly always on one or other limb, often beginning on the pads of the feet, but it may start anywhere, and, from the position assumed in the cage or water, the first noticeable ulcer is on the upper or lateral aspect of a hind limb (Pls. I., II. figs. 4 & 5). The ulcer is at first small, but as it extends it causes a weeping of the skin in the neighbourhood, and the outpouring of fluid carries down the fragments of mould and so spreads infection to other parts. After a time, usually two weeks or so, the ulcers may thus become more or less generalized; they do not, as a rule, become confluent over a large area, but several areas appear to be involved in rapid sequence, if not almost simultaneously. An explanation of this is suggested later under the section dealing with Pathogeny. In the case of the Salamander this extension is not, as a rule, met with because death occurs from sepsis before it has time to develop.

Yet a third train of symptoms may be encountered, and this is quite common in Bull-Frogs and in Square-marked Toads. After the primary ulcerous lesion, instead of a generalized cutaneous outbreak, the initial sore may heal or remain fairly stationary. The respiration-rate, however, is found to alter, becoming increased, and the body generally is noticed to become larger and appears distended. This swelling of the body increases and the respiratory rate steadily goes up. The appetite is lost and the animal is obviously distressed. Towards the end—and when once it passes the primary stage unchecked the condition seems invariably to terminate fatally—the swelling of the body becomes more marked and the respirations very rapid and laboured.

It is highly contagious; if one affected Salamander, for example, is placed in a vivarium with several others free of the disease and in a cage which has been thoroughly cleaned, disinfected, and furnished with fresh sand and mould, the rest will soon exhibit lesions in the same situation (the nose), and on examination each so attacked will show the presence of the hyphæ.

### Pathological Anatomy and Histology.

A detailed account of the changes set up in various organs will be given in the succeeding paragraphs. At the present juncture

a brief statement of the *macroscopic* appearances may be made. Ulcers, some in an active condition, some healed, may be seen, usually on the hind limbs, and the whole body is swollen, bloated, and abnormally pale. On opening the body the viscera are seen to be bathed in a clear, thin, watery fluid. The peritoneal cavity shows ascites, as much as 4 oz. being measured in one instance, $3\frac{1}{2}$ oz. in another. This is probably the result of the cirrhotic state of the liver, as is seen in Man with Laennec's type of multilobular cirrhosis. Hydrothorax and hydropericardium are also present, partly due to heart failure and partly secondary to the renal fibrosis. One's attention is immediately struck by the large size of the liver, kidneys, and spleen as compared with the normal, as well as by their toughness and streaked or mottled appearance, resulting from infiltration with the growth.

The normal measurements of the liver, spleen, and kidneys in a Bull-Frog are given below, and the measurements in two cases dying from this disease.

| Organ. | Normal. | Case I: Death-Book No. 459/25. | Case II: Death-Book No. 788/25. |
|---|---|---|---|
| Liver . | 6·25×4 ×1·75 cm | 10×8 ×4 cm. | 12·8×8·4×3·8 cm. |
| Spleen ... | 1·20×1 ×0·5 „ | 2×1·5×1 „ | 2·0×1·6×1·2 „ |
| Left Kidney | 3·0 ×1·75×0·9 „ | 7×4 ×3 „ | 5·9×3 ×1·9 „ |
| Right Kidney | 3·0 ×1·5 ×1·0 „ | 6×3 ×2·5 „ | 6·5×3·4×2·5 „ |

It will be noticed that each of the organs attains a size almost twice the normal in all dimensions.

The individual lesions may next be described in more detail. There is nothing peculiar in the initial ulcer macroscopically. It is not, in the earliest stages at least, a deep one; it appears to present a fairly clean-cut margin, but on closer examination the border is found to be undermined (Pl. I. fig. 4). If a little of the discharge and the débris from beneath the edge is examined fresh, septate hyphæ are found in varying amount and in many instances active nematode larvæ (Pl. II. fig. 6). On staining, the hyphæ are brought out more clearly, and if a culture be made on Sabouraud's medium with maltose a wrinkled white growth appears in the course of five days, or even less, and spreads until a large surface of the medium is covered, the central part being white, wrinkled, somewhat crateriform, as shown in Pl. II. fig. 7.

Microscopically, the skin near the ulcer is usually found to be quite healthy on the surface, but where this is denuded, that is at the site of the ulcer itself, there are seen to be hyphæ spreading in practically every direction. In the very early stage (Pl. III. fig. 8) a penetrating hypha seems to enter by a lymph-space, and others lie in a lymph-space beneath the epidermis.

Thence it seems to spread in all directions, destroying and replacing the tissues. The mould forms a dense feltwork beneath an ulcer where the skin has been removed. The growth is so dense that it is hardly possible to determine whether it extends now by way of the lymphatics; we see mycelium, spores, and hyphæ in all directions, and the latter sprouting from the former.

When denser structures are encountered, such as tendon or muscle for example, the hyphæ, as one would expect, tend to run along the fibres, and they seem to produce more spore-formation.

Mention has been made of the pallor of the skin of the animals attacked (Pl. I. figs. 2 & 3), and in view of the work of Dr. Hogben* on the action of the hypophysis in leading to albinism, this structure was removed carefully from some of the animals dead of this disease and serial sections were made, but in no case was there any trace of hyphæ detected. The hypophysis appeared to be perfectly healthy.

*Glands.*—The lymph-glands are often much enlarged; they have been met with as large as a cobnut, slate-grey in colour and unduly tough. On microscopical examination there is generally no sign of hyphæ breaking through the capsule; fragments of them are seen in the subcapsular lymph-spaces, but not in the capsule itself unless the gland is so densely involved that little lymphoid tissue is left. Under these conditions the capsule may be, as it were, split, and hyphæ may be seen running beneath the surface. In the interior, however, the growth is more marked and dense than towards the outer parts, and if examined before the mass is too crowded the hyphæ appear to lie in clear spaces which may be lymph-spaces and sinuses. The gland-tissue shows signs of attempted resistance. Thus, giant-cells are much in evidence, and Murray's stain serves to show excellently the giant-cell formation round the tip of a growing hypha or round a spore; in other parts the reaction has progressed even further to produce a marked fibrosis.

Some peculiar structures are seen in the section, the nature of which I cannot even conjecture. Some are cut transversely, others sagittally, others again longitudinally. Those cut transversely reveal best the minute structure, as in Pl. III. fig. 9. There is seen to be a granular internal core around which is a very definite layer, in some cases apparently hyaline, in others radially striated, with a highly refractile periphery. External to this is a layer, circularly laminated, granular in general aspect, but interspersed with cells disposed in three or four strata and following very closely the contour of the structure immediately interior to it. Outside this again is a more condensed stratum, also granular under high magnification, and external to this a second laminated layer similar in general structure to the first, but showing a more definitely circular stratification. Between

* "The Pigmentary Infector System. A Review of the Physiology of Colour Response." L. T. Hogben: 'Biological Monographs and Manuals.' Oliver & Boyd: Edinburgh, 1924.

this and the somewhat condensed or compressed tissue of the gland is a clear space which is probably the result of shrinkage in preparation of the specimen.

Several suggestions have been made as to the nature of these bodies: That they are helminths; that they are concretions; that they are sections of hyphal growth; that they are plant hairs. The first cannot be maintained for a minute, the structure is quite unlike that of any known helminth; prolonged treatment with acid-alcohol does not affect any material change in them, and the cellular structure is very definite, so there is not any support for the theory that they are concretions; they may be abnormal forms of hyphal growth, for they stain, in part at least, similarly to the hyphæ elsewhere, but, whereas hyphæ are abundant in the organs and tissues attacked, these bodies have been rarely met with, though fortunately fairly numerous in the tissue from which the microphotograph has been made. This is exceptional, and in no other of the animals dying from this disease and whose tissues have been submitted to minute histological examination has there been any sign of them. Lastly, it has been suggested by Professor M. J. Stewart, of Leeds University, to whom I sent some sections, that they are vegetable hairs. Evidence in favour of this is that they were found in but one animal, that they were very limited in distribution, being found only in the submucous layer of the intestine and in a mesenteric gland. This very distribution affords support to this opinion; but, on the other hand, the hair must be very firm to have thus penetrated, and no such hairs can be found in the enclosure which this animal inhabited. It is, however, conceded by all who have seen the sections that these bodies have probably nothing to do with the disease condition, so we may dismiss them from the present account.

*Spleen.*—This need not be described in detail; the conditions are exactly like those in an infected lymphatic gland—increase of fibrous tissue, the presence of hyphæ and giant-cells being particularly prominent (Pl. IV. fig. 10).

*Lung.*—In none of the animals examined is this organ at all extensively involved. Even where it is affected there is no naked-eye change and the condition is only discovered microscopically; hyphal fragments are seen in the alveoli and the thickened alveolar walls, the former often being filled with shed epithelial cells. Whether the condition attacks the walls first or the lymphatic paths in them and thence extends to the alveoli, or, *vice versâ*, the alveoli by inhalation, is a question which naturally arises; but seeing that the hyphæ are very rare, usually absent, from the bronchioles, the general impression supports the former view. Also, from the absence of hyphæ or spores in the arterioles it may be inferred that the spread is not by the blood-vascular route.

*Intestine.*—Though many sections have been made from different parts of the alimentary canal in various animals dying from this

mycotic disease, no hyphæ have been found*. In fact, the only abnormality seen was in the submucous layers in one Bull-Frog, where sections of the peculiar structures already described as present in the gland were met with.

*Pancreas.*—In the parenchyma of this gland, in advanced stages at least, hyphæ are found in fair abundance, but more appear to be situated in the islets of Langerhans than in the gland-tissue proper. Rarely is a hyphal fragment seen in a blood-vessel, and still more rarely in a duct. In parts, especially at the periphery, fibrous tissue is in excess, and here, in some situations, there are signs of penetration by the mould, but whether this can be interpreted as indicating direct extension from without there is not sufficient evidence to decide with certainty.

*Liver.*—The parenchyma is greatly disorganized, so much so that in many parts of the section it is far from easy to recognize that we are dealing with liver at all. Some hyphæ may be seen in branches of the portal vein, fewer (sometimes none) in the hepatic artery, very rarely at all in the bile-ducts; in fact, so few in the last-named that many fields may have to be examined to find one, and it is possible that they may have been displaced thither in cutting the section.

Throughout the liver generally there is much increase of fibrous tissue; in fact, in one specimen which was mounted permanently three or four years ago and to which I have already referred, the condition was labelled cirrhosis of the liver.

In the region of the capsule, hyphæ may be abundant, and in one or two situations they may appear to be breaking through. To decide whether we are to interpret this as extension from without or from within the following points may help:—The growth of hyphæ is more abundant in the interior of the liver (Pl. IV. fig. 11): hyphæ are rare, or even absent, in many sections of parts just below the capsule; the peritoneum is not involved, or only very exceptionally. On the other hand, it might be argued that the growth might find an obstacle in the fibrous capsule, but when once it had penetrated at one or more spots growth through the less resistant parenchyma would be more exuberant. In other sections the capsule appears to be densely infiltrated with growth, but not at the actual external surface; the impression given is rather that from the liver tissue extension has occurred through the inner aspect of the capsule, and thence a more widespread dissemination between and amongst the fibres of the capsule (Pl. V. fig. 12).

*Kidney.*—As in the case of the liver, the renal tissue is greatly disorganized, and there is marked fibrosis. The parenchyma is infiltrated in all directions, so that in parts the tubules are barely recognizable. At the same time it is a remarkable fact that the tubules themselves rarely show any hyphæ; these appear to be interspersed between the tubules and in the fibrous tissue. As

* Later examinations have revealed the presence of an occasional hypha.

in the liver, the outer layers of the capsule do not show hyphæ in any considerable amount, but it seems to have been split, as it were, by extension from within, the growth then taking place parallel to the surface. Also, the glomeruli frequently escape. In parts one may see abundant growth amongst the tubules, with fibrosis and disorganization, but glomeruli show no mould; in other parts (Pl. V. fig. 13) the glomeruli are seen not to be entirely exempt; in the upper part of the field is an intact glomerulus, below is one showing a fragment of the mould, and partial destruction of the tuft; a little lower still, but too distant to be included in the field, was a glomerulus which had been converted into a fibrous nodule. This, however, is exceptional. Occasionally in the kidney also may be seen giant-cell formation round a mycelial point.

As regards other parts of the body, although the animal died of the infection, and the liver, kidneys, spleen, lymph-glands, skin, and subcutaneous tissues were densely invaded, no sign of any mould could be found in the alimentary canal, heart, brain, or nervous system generally, the fat-bodies, ovaries, or spawn.

*Pathogeny.*—Having described in detail the macroscopic and histological changes found, we may briefly consider the pathogeny of the condition. There can be no doubt that the initial lesion is in the skin. At a time when the animal appears to be in perfect health, except for the presence of a small ulcer with its undermined edge, a smear taken from such a ulcer shows the hyphæ of this mould. If local treatment be energetically undertaken at this stage cure can be brought about. A point worthy of consideration is whether the lesion is made by the mould being introduced somehow into the healthy skin, or whether some small abrasion permits the fungus to obtain a footing. It has been stated that examination of the discharge reveals not only the hyphæ but larval nematodes (Pl. II. fig. 6). Larval nematodes in the filariform stage can penetrate actively the skin of a mouse, as has been shown by Dr. Goodey's experiments. The nematodes in this disease, however, are not filariform but rhabditiform. Such have not, so far as I am aware, ever been shown to be able to penetrate the unbroken skin. Do these helminths play an essential rôle in introducing the mould?

The following are the main points in favour:—(1) The larvæ are found in the ulcer in nearly all instances. (2) Inoculation, even in large amounts of a pure culture of the mould does not produce the disease in a healthy animal when applied to the intact skin, to a scarified surface, or subcutaneously. (3) Larvæ of some nematodes can penetrate (v.s.) healthy skin.

On the contrary:—(1) The larvæ are not *invariably* found, but it is quite possible that they have been present and have later been washed away by the discharge or have betaken themselves elsewhere. (2) Examination of sections of the underlying tissue does not reveal any such parasites. (3) No spores or fragments of hyphæ have been seen in any of these larvæ. (4) In analogous

conditions, as the Mucor infection of Lizards, no larvæ have been seen at all.

We must not forget to mention, however, that even if absent at the time of examination, they may have served their purpose in producing a local lesion and allowing the mould to gain a footing and penetrate; or, since inoculation of a culture alone has not succeeded, they may have prepared the soil by their secretions or by local toxic action, and that in the absence of this a healthy animal with an accidental abrasion may, even if attacked by the fungus, be able to resist and throw off the invasion. In default of positive results from experimental work this question must for the present remain unsettled.

The next point is the mode of penetration. Examination of many sections of healthy skin in a grossly infected animal has failed to reveal any penetrating hyphæ (*i. e.* actually perforating the skin). If there is an abrasion and ulcer, there is obviously every chance for such an aggressive organism to enter. Where the skin is healthy, any hyphæ present are seen to be in the deeper layers, and appear to be traceable from those which have entered at the site of a neighbouring ulcer, and have, on reaching the dermis, spread in all directions. If seen at all where the epidermis is apparently intact, the hypha seems to be entering in a clear space, a lymph-channel (Pl. III. fig. 8), which channels communicate at intervals with the surface in a frog's skin.

After penetrating beneath the surface, its mode of dissemination may be by the blood-stream or by the lymph, and the evidence is vastly in favour of the latter. In the first place, we rarely find the mould in blood-vessels. Thus, in the lungs, hyphæ are rarely seen at all; in the kidneys the vessels are nearly always free, even when the whole organ is so attacked as to be barely recognizable; the same applies to the liver. In the heart I have never seen the hyphæ, nor in any part of the central nervous system. The clinical history is quite definite of a local sore, a period of quiescence, and then a more generalized outbreak with swelling of the abdomen, panting respirations, etc., as already detailed. This might be explained by the lymphatic route of entry, penetration to the lymph-sinuses, and extension upwards from below, or a checking by the lymphatic glands which, as we have seen, become densely infiltrated, and then a spread to the various organs by the lymphatic channels. This would also explain the intertubular disposition of the mould in the kidneys and the escape of the blood-vessels, also the absence of it from the vessels of the pancreas, although the hyphæ are found in the parenchyma, but not the ducts; the liver, though more vascular and very heavily infected, shows comparatively little involvement of the vessels, and this may be explained by direct penetration which can be seen in some sections. Again, in the earlier stages of lymphatic-gland involvement, the hyphæ are found more abundantly in the subcapsular lymph-spaces, and only later throughout the gland-tissue itself.

In conclusion, a fungus so malignant certainly deserves a label. Culture shows that it is definitely a *Monilia*. A subculture was sent to the Mycological Section of the Molteno Institute for Research in Parasitology, at Cambridge, and Dr. J. G. Hare has informed me that, though a *Monilia*, its manner of growth is peculiar and does not correspond with any of the known species. Since it has been isolated from so many of the Batrachia, as stated in the introductory remarks, but has not been found, so far at least, in other animals, I would suggest the name *Monilia batrachea* as suitable, deriving the specific name from the Greek βατράχεος, since the alternative βατράχειος has no distinctive feminine.

## EXPLANATION OF THE PLATES*.

### Plate I.

Fig. 1. Photograph of the ventral surface of the healthy Bull-Frog (*Rana catesbiana*), showing the normal degree and distribution of pigmentation.

2. Photograph of a Bull-Frog in the intermediate stage of the disease. The surface is whiter than normal and the abdomen beginning to enlarge.

3. Photograph of a Bull-Frog dead of the disease. The pallor of the skin is marked, and the general œdema of the limbs and the enlargement of the abdomen are well shown.

4. Photograph of the right hind-leg of a Bull-Frog, showing the ulcers in an early stage, with a punched-out appearance but slightly undermined edge.

### Plate II.

Fig. 5. Showing the ulcers at a later stage, but before the disease has extended in the viscera. Note the large ulcerated surface due to confluence of smaller ulcers and not to spread of a single one, and two smaller ulcers below, which in a few days will join up with the large.

6. Smear made from the discharge beneath the edge of an ulcer, showing a nematode larva. The darker mass is made up of matted mycelium, individual hyphæ being seen at the periphery.

7. Photograph of a culture of the fungus grown on Sabouraud's maltose medium, 7–8 days old.

### Plate III.

Fig. 8. Section of skin, showing a hypha penetrating *via* a lymph-space. Below is a larger hypha lying in a space.

9. Bodies, (vegetable hairs, in section of a mesenteric gland. The tissue is unstained in order to show up the transversely-cut bodies more clearly.

### Plate IV.

Fig. 10. Foreign-body giant-cells round hyphal fragments in a section of spleen. The glands show a similar condition.

11. Section of liver parenchyma, showing the extreme dispersion of the septate hyphal growth. The liver-tissue is recognizable only in certain parts of the section, the destruction and replacement by mould-growth being very great.

### Plate V.

Fig. 12. The edge of the liver, showing the mould apparently breaking through from the interior into the deeper layers of the capsule and then growing parallel to the surface.

13. Section of kidney, showing two glomeruli. The upper is normal. The lower is considerably altered; hyphal fragments and spores are present, and the lowest part is fibrotic. A little below this again, but too distant to be included in the field, was a third, completely fibrosed and showing in its interior small hyphal remnants.

* The photomicrographs have been made by Mr. F. Martin Duncan, the others by Mr. F. W. Bond, to both of whom I wish to express my sincere gratitude.

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ON THE MASSING OF THE LADYBIRD
(*HIPPODAMIA CONVERGENS*)

# 32. On the Massing of the Ladybird, *Hippodamia convergens* [illegible] Yosemite Valley. By Onera A. [illegible] F.E.S.*

[illegible] 21, 1926: Read June 15, 1926.]

(Plate I.†)

CONTENTS.



## INTRODUCTION.

When I reached the Yosemite Valley on October 28, 1925, I immediately made enquiries from everyone I met whether they had seen any ladybirds (*Hippodamia convergens*) in large numbers. At the end of an hour I found a waggoner who directed me to a field in which a group of Azaleas were growing (see foreground of Pl. I. fig. 1), near which he had seen large numbers of ladybirds. He had been digging in a pit near by for the last four or five weeks and had seen the insects on the wing for a couple of hours in the middle of sunny days.

On reaching the group of leafless Azaleas, I found the spot sunless and cold, for the high cliffs had already, at 2.30 P.M., hidden the sun. The Azalea is indigenous in the Sierra Mountains at an elevation of 3500 feet. The air was destitute of ladybird-life, but among the dead leaves under the Azaleas I found eighteen masses of *Hippodamia convergens*. They were well hidden under the leaves and nearly always grouped around the base of a stem, but there was not time to find if there were more groups before twilight suddenly came.

Each group of insects was congregated into a ball-like mass the size of one-half to one fist in bulk. I shall follow the example of the woodmen, and call the spot in which each group lay a nest. There was a complete segregation of nests, not a continuity of ladybirds along the whole area. The social instinct that makes the ladybirds collect together is so strong that there were no stragglers between the masses, but the social instinct

* Communicated by Mr. E. Ernest Green, F.Z.S.

† For explanation of the Plate, see p. 705.

was not, at that particular time, strong enough to make all the masses into one.

The condition in the Yosemite may be compared with that in a very narrow canyon on the side of Mount Tamalpais, near San Francisco, where Dr. Van Duzee very kindly took me to see a small massing of *Hippodamia convergens*. The several groups which had collected in some brush by the side of the road were disturbed in the late afternoon of October 25, 1925, by turning the brush over, in order to see how the ladybirds would reassemble. A number began at once to climb up the main stem and collected at the very top, where some remained. Others also came up gradually, and pressed as near as possible to the first settlers, still more followed, and the latest comers crawled on top of those already assembled. Finally, the mass was so top-heavy that gravity became a greater force than the social instinct, and the top part of the mass toppled and fell. In the meantime, other centres of population had started in various parts of the bush, but the important point is that, when we left, there were more nests in this reassembling than there had been before we disturbed the insects. If we had returned the next morning or afternoon, would there have been a reduced number of nests because the social instinct would have had more time to act? It would be interesting to know what characteristic in some particular ladybird, at some special situation, served as the force which started each nest: was it the member of one sex rather than the other, a ladybird with a particularly strong odour or some other attribute?

In the Yosemite I marked the position of a number of the nests by pieces of yellow paper pinned on a branch above the nest, in order to find the ladybirds after dark.

The floor of the valley where the massing took place has an altitude of approximately 3960 feet, and an average width of only a mile. The Azalea bushes were near the base of a cliff which extends almost perpendicularly, 3254 feet high above the valley. The altitude of the top of the cliff is therefore 7214 feet. In Pl. I. fig. 1, groups of trees can be seen on the mountains above the valley, but so far, no ladybirds have been found hibernating there. In this case, the ladybirds have chosen for their winter-quarters the valley and not the highest possible point.

## Experiments at Night with Light and Heat.

The night experiments planned had to be made on masses which had not been disturbed in the late afternoon. If the ladybirds were disturbed in the smallest degree they moved about in the immediate neighbourhood, and took one to two hours at least to settle quite quietly again. I wished to try the effect of light and heat, separately, upon the insects, about 9 P.M., when it was dark. The moon was bright and nearly full, eleven days old, but its light had no stimulating effect upon the movements

of the ladybirds. Under the Azalea bushes it was comparatively dark. The light of the moon is only a fraction of a candle-metre, but I understand it is sufficient to make bees restless at Rothamsted Experimental Station.

The pieces of paper could be seen a yard away in the moonlight, so the nests were soon located.

We lay upon the ground that the heat of our bodies might not affect the ladybirds. I held the torch, parallel to the ground, the axis of the light passing above the leaves under which the nest was hidden. The lens of the torch was four inches from the centre of the group of ladybirds, but shining only on the leaves that covered them. A companion counted the time, and in half a minute the ladybirds began to move; they did not move either straight towards or away from the light, but up the trunks of the Azalea bushes--they were neither positively nor negatively heliotropic. During the two evenings only one ladybird walked on the glass of the torch. The ladybirds collected on my hat, and several were found, three feet from the mass, on my coat. It was impossible to tell how far, if at all, they went beyond the bushes. At the end of twenty minutes no live ladybird was left under the leaves. All the ladybirds, so far as it was possible to see, were walking, none were flying.

It was impossible to tell how much light penetrated through the dead leaves or even to test the illuminating power of the torch in metre-candles, but I have since tested several torches which were supposed to be the same and found they varied from 2·3 to 5 metre-candles.

The heat produced by the torch is very small. In a laboratory, where the air is comparatively still, when the lens is placed at a distance of $\frac{1}{4}$-inch from the bulb of a thermometer, the heat produced raises the temperature $0^{\circ}\cdot4$ C. at the end of five minutes and $0^{\circ}\cdot8$ C. at the end of ten minutes. At a distance of four inches, the distance of the lens from the nest in the original experiment, there is no effect on the thermometer even at the end of twenty minutes. In the open air the results would be even smaller. It is safe to state that the electric torch produced no heat effect upon the ladybirds.

It has to be remembered that, even by day, the sunlight falls on the leaves, but not directly on to the nest of ladybirds which are hidden away underneath.

The same experiments were repeated with other nests, but with the same results. On my way home I was aware that ladybirds were walking on me, and I caught about thirty in my clothes.

W. B. Herms and Martha S. Beaser (1) write, in an unpublished paper, that, in *Hippodamia convergens*, "The reactions to light are positive, but the light stimulation seems to cause an increased movement and a reaction causing dispersal rather than assembling." I made no observations on the reaction of light to assembling.

I then tried the effect of heat upon several nests. A frying-pan was heated over a tin of solid alcohol until the pan felt very hot to the finger, and the pan was then held upside down over a nest. At the end of two minutes I heard something knock the underside of the pan, and, on looking with a torch, a number of moving ladybirds were seen on the stem and adjacent leaves. Again, the ladybirds were walking up the stems. They did not move as a whole directly to the pan. At the end of ten minutes they were not as far up the stem as after ten minutes' stimulation with light. It was impossible to look often or for more than a second for fear of complicating the results by light stimulation.

The only thermometers available were one from an hotel and a clinical thermometer, and both were useless. Since my return to England I have repeated the experiment with a pan of the same size, raised to what I judge was the same temperature. By this means I found the temperature at the level of the covering leaves must have been approximately 23°·5 C., a temperature which, judging by the observations carried on during the day, would be expected to cause some movement. It was impossible to keep a steady temperature, but the pan was periodically re-heated.

With heat alone the movements were not as great as during the day with the combination of heat plus light. This confirms my observations on ladybirds living in boxes, where I have found that sunlight plus a lower temperature caused greater movement than a higher temperature without direct sunlight.

Herms and Beaser, in the paper quoted above, say, "Thermal reactions exert a powerful influence, as evidenced by the fact that the beetles assembled in the fields and the laboratory in small and increasingly larger groups as the temperature is lowered, and disperse again as the temperature is raised. The temperature at which *Hippodamia convergens* is caused to assemble is 28° C."

The following night the same experiments were repeated with similar results, but experiments were also made on ladybirds which were in the crevices of the bark of a yellow pine and also in a hollow at the base of its trunk.

The ladybirds were closely packed together, the head being directed towards the centre of the tree, so that, looking into a crevice, only the red elytra could be seen. This may be a device to hide from stimulus the sense-organs which would be affected by light and, perhaps, heat too. Dr. Essig allows me to publish a photograph of *Axion phagiatum* hibernating in empty acorn-cups, in which the ladybirds are in the same position. *Adalia bipunctata*, when hibernating in England, tends to take up the same position. Evidently this position is not an isolated phenomenon and probably has some biological importance.

The trunk of the tree was completely in shadow during the day. None of these ladybirds had been on the wing, and those in the crevices had not shown the slightest sign of movement. In a shallow hollow at the base of the tree there were a large

number of ladybirds. Those deep in the hollow were in the same position and as quiescent as those in the crevices higher up the tree, but those on the outer parts of the hollow were moving about slowly.

The torch used the second night gave a considerably brighter light than that used the first night. When the light was passed across the crevices there was no movement, and yet a much larger amount of light must have reached the ladybirds than through the leaves which covered the masses on the ground. Even at the end of twenty minutes there was no movement; evidently the response of the crevice ladybirds was different to that of the ladybirds under the Azalea bushes. The light was then directed full at the ladybirds, but there was only a slight movement even at the end of fifteen minutes.

The response of the ladybirds which were not quite in the hollow at the base of the tree was different. The application of both heat and light made them move, and at the end of fifteen minutes some were found crawling three feet up the tree-trunk but, again those deep in the crevices of the hollow were far less sensitive to light, and even after twenty minutes of direct light at a distance of only two inches none of them had moved.

The heated frying-pan was useless on the tree, so the ladybirds were warmed by breathing upon them very gently. After five minutes a few in the outer parts of the crevice moved. When warming by breathing, three other factors besides warmth are introduced—a current of air, moisture, and carbon-dioxide.

The ladybirds in the crevices of the tree were more responsive to warm breath than to light, but there is no evidence to show how much the other factors had to do with the response. It seems as if these ladybirds had sunk into a condition from which they were less easily roused than those under the Azalea bushes which, until that date, had had a few hours of flight on sunny days; here there is the appearance of a cycle of differing physiological conditions comparable with that of hibernating mammals. If the insect passes into such a condition that it no longer responds to the stimulus of the occasional warm day during the winter and to the brightness to which they would be exposed after an unexpected mid-winter thaw, they would surely be better able to survive the long hibernating period. The sun-dance must be a serious menace to survival, as it certainly uses up a considerable amount of the fat or whatever substance is stored up. So far I have been unable to get any information as to whether there is greater mortality when hibernation is interrupted by a number of sunny days than when winter comes and stays without intermission.

These simple and crude experiments make it quite clear that ladybirds react to pure heat and pure light stimuli. Under normal conditions there is light plus heat, and it remains to be found which plays the bigger part and what is the optimum condition for each. The experiments of the second night

suggest that the rapidity of response to both these stimuli varies considerably with the physiological condition of the ladybird. It depends upon the length of time the ladybird has been hibernating and the time it last responded to the stimuli of heat and light.

At 5.30 P.M. in the afternoon the whole of one mass, as far as I could see after careful examination of the site, was removed eighteen inches from the nest out into the open. At 8.15 P.M. there was a steady stream of ladybirds making their way back to the nest, but few had reached it. At 9 A.M. the next morning the mass was apparently complete again in its nest, and no ladybirds were on the road.

The individuals of this nest, during the hour that I watched them, showed no tendency to walk to several other nests which were within a radius of one foot from the disturbed group. If it had been possible to mark the ladybirds, one could have been sure of the results. It is certain that this procession homewards to the nest was not directed by either heat or light. I should have liked to try artificial solutions of the substance which produces the characteristic odour of the ladybird, for the obvious deduction is that they found their way back by the scent. Herms and Beaser remark, however, "They do not react either in the field or in the laboratory to their own odour or to artificial odours, so that odours seem to play no part other than that of protection and, without doubt, in sexual attraction." Ernest Crabbe has made solutions of ladybirds in the hope of thus collecting quantities of ladybirds, but the solution did not act as a special attraction.

Ladybirds had certainly hibernated under these Azaleas for a number of winters, for digging brought to light faded elytra three inches down in the decayed leaf-mould. These ladybird cemeteries were both under the modern nests and also at spots where, on those two particular days, there were no nests.

There are many instances of ladybirds, of various species, reassembling for a succession of years either continuously or interruptedly in the same situation: *Adalia bipunctata* in a top room in a house at Bournemouth, England; *A. bipunctata* in the same trees at Esher, England (observed by H. J. Burkill); in the same houses at Sutton, Surrey, and North Cray, Kent (observed by G. B. C. Leman); *Coccinella septempunctata* and *A. bipunctata*, the two species in segregated groups, under the bark of larch-poles at Ripley, Surrey (observed by G. Fox Wilson); *Hippodamia convergens*, among grass, at Horse-Tooth, near Fort Collins (observed by Miriam Palmer); *Semiadalia*, on a certain height above Nancy, France; *A. bipunctata*, *C. septempunctata*, and *Semiadalia*, on the summit of Puy-de-Gergovia, in Auvergne, France (observed by Professor Eusebio) (3).

This use of the same place by the same species is not confined to Coccinellidæ; Scott (2) states that certain *Chloripidæ* come to the same room, in England, time after time. This statement is

confirmed by a considerable amount of data collected by Dr. Gahan at the Natural History Museum at South Kensington, London. These flies do not hibernate in the rooms, but they do assemble in enormous quantities.

The Monarch Butterfly, *Danais plexippus*, assembles in large numbers in the autumn, and it is stated that it collects year after year in the same places in California.

The basal fact in all the cases, and only a few are enumerated, is the selective assembling, whether for migration or hibernation. The insects collect together in pure or nearly pure groups, just as birds do; they are not, to any appreciable extent, mixed with other insects of the same neighbourhood, and when there is a mixture it is usually with an allied insect. This also is the case with birds, where, in a flock of Chaffinches there may be a few Sparrows and a few Greenfinches. Such assemblings cannot be regarded as due to such a physical cause as an air-current, but must be the result of some biological force such as the reaction due to the presence of certain sense-organs. When the biological assembling has taken place, then an air-current may have important effects as a distributor.

### Observations on *Hippodamia convergens* during the Day.

The Yosemite Valley, on the southern side where the ladybirds were found, is in deep shadow for a large part of the day in late October.

In the morning an ordinary thermometer was placed on top of a nest, supported on sticks so that there should be no mechanical disturbance of the insects. At a temperature of 63° F. in semi-shadow, the ladybirds were quiet; at the same temperature, but when there was a considerable increase in light but no direct sunlight, the ladybirds began to move, but when the sunlight was on the bushes and the temperature had risen to 70° F., some of them were flying in the air and there was general movement in the nest, but it is important to notice that while some individuals were flying, apparently with much excitement, others were merely crawling and a few were quite still, although not dead. There was, in fact, individual behaviour as well as an average tendency to certain average behaviour.

When, in direct sunlight, the temperature had reached 80° F. the nests were nearly deserted. The maximum temperature in the sun that day was 94° F. In every case the thermometer was placed on the ground, but the real temperature of the air, five feet above the ground, where the ladybirds were flying would be considerably less. It may perhaps be even as much as fifteen degrees less than the maximum temperature of 94° recorded by the thermometer, for on account of radiation the temperature indicated by the thermometer is not that of the air.

There appeared to be more excitement, as evidenced by rapidity and irregularity of flight, as the temperature rose towards 74° F.

than when, after a maximum of 94°, it sank again to 74°. This may have been due to muscular exhaustion or because the maximum stimulation had been received, and there was a physiological reaction of the same kind as that known in the higher animals. When the sun had gone and the temperature had sunk to 54° F. all the ladybirds had retreated under the leaves, except a few which will be mentioned later.

The Azaleas were on a narrow patch extending approximately east and west; the sun first fell on the eastern end, and there the insects deserted their nests and flew in the air when the necessary degree of temperature and light had been reached, and as its rays moved along the patch one mass after another arose. The sun seemed to pass along the Azalea town, knocking in succession at the doors of each house and awakening the inhabitants. At one time the temperature in the sun at the eastern end was 84° F. and in the shadow at the other end only 63° F.

The ladybirds did not fly in the air unlighted by the direct rays of the sun, and as the path of the sun's light moved along, the ladybirds kept in the lighted zone, like the prima donna who keeps always in the limited area of the spot light. The ladybirds were as much confined to certain limited aerial spaces as if they had been surrounded by stone walls. With such limited and definite response to the stimulation of light, there was no chance for them to migrate far. Ladybirds which hibernated on mountain-tops or in other well-lighted positions would not have their daily movements so confined. As the sun sank the ladybirds began to return to their nests, but I had no paint with which I could have marked the insects and so find out whether they returned, in the late afternoon, to the same place which they had left a couple of hours before. It seemed to me that there was an increase in the size of the groups nearer the place where the sun had last shone. Sixteen of the eighteen groups marked were re-formed, but two situated at the east end, which was first warmed and first cooled, had no ladybirds at night.

These observations show that very enlightening and interesting results concerning the tropisms of the ladybird might be obtained by a worker, with adequate apparatus, who could devote a considerable time to experimentation and observation in the field.

### Reactions to Food.

I knew by experience in England (4) that *Adalia bipunctata* would eat dates with avidity, so I tried *Hippodamia* with the only two likely foods I had—orange-juice and split raisins.

There was little or no interest in the orange-juice. A few ladybirds lapped at the juice when it had nearly dried on the twigs, but they did not stay long.

The split raisins were put near nests when the ladybirds showed signs of movement. At the end of an hour most of the raisins could not be seen, but their position could be recognised

by the crowd of red ladybirds which completely covered them. During the day there was a constant coming and going of diners, some remained only three minutes, but two, at least, stayed for five minutes. Even when dusk had come and the temperature had fallen to 54° F., two to four ladybirds remained on each raisin, although the majority of the ladybirds were sheltering under the leaves. On returning at 9.30 P.M., when the temperature was 42° F., there were still two ladybirds on one raisin, but by the next morning they had disappeared. The stimulus of the food was stronger than the tendency to retreat into shelter on the coming of darkness and cold.

There were certainly no aphids for the *Hippodamia* to eat, but they apparently had drinks from the fine film of moisture which covered the Azalea buds or from the minute drop of dew in the forks of the branches. I do not know if the fluid on the buds contained any dissolved albuminous matter or whether the ladybirds ate any of the fine hairs which outline each of the scale leaves.

Clearly some of the ladybirds were willing to eat if given the opportunity, but there was no wild starvation rush to the sugary raisin. The movements of the ladybirds towards the raisins did not appear purposeful, but, as I have observed so often before, the insect seems to find its food merely by wandering and not by any directive instinct. Perhaps the time will come when we shall be able to find the means by which the ladybird and its food are brought together. It seems biologically unsound that the ladybird should just happen on its food, and yet the spider lives successfully by merely sitting still until the fly, apparently, happens into her web.

## Altitude and Hibernation.

Several other massings were reported in the Valley, but I did not have time to locate them.

As far as I could learn, the ladybirds hibernated in the Yosemite Valley and not on the surrounding mountains, but in such a great area very little is as yet known. A number of authorities now believe that canyons and valleys, rather than mountain-tops, are the usual position for hibernating in the Sierra Nevada Mountains of California. The mountain currents, either hot or cold, are very strong and well defined throughout the Sierras. They are indeed so limited that even the unscientific and unimaginative mind realizes them as definitely as if they were visible streams of water.

Over the Yosemite Valley the currents are so strong that aeroplanes are not allowed to land in the valley. How far these currents of air affect the movements and hibernation of ladybirds is an interesting and debatable question.

At some places in the Rocky Mountains the ladybirds are found on the highest points, but the only place of this kind that

I visited was Horse Tooth Mountain, 7160 feet, in northern Colorado, on the eastern side of the Rockies. The Horse Tooth is an isolated bare mass of rock, and has growing on it, here and there in its rough crevices, small tussocks of grass with from one to six inches of soil underneath. Miriam Palmer and George List, of the State Agricultural College of Fort Collins, reported that numbers of *Hippodamia convergens* had been repeatedly found hibernating on this height. We went there on November 21, 1925, and, although there were no living *Hippodamia*, there were elytra of dead ladybirds on or in the soil even when the tussocks of grass grew in the most exposed positions possible. A few elytra, the red considerably faded, were found two inches beneath the soil. Periodically the ladybirds had come and some dead were left behind.

Fig. 2 shows the eastern range of the Rocky Mountains with the Horse Tooth as the highest point. The foreground, 4994 feet, is the edge of the great plateau which stretches across the American continent.

The contrast between the conditions of the hibernating *Hippodamia* here and in the Yosemite Valley, as regards situation and altitude, is extreme. In both places the insects would pass some months under the snow. In the Yosemite the ladybirds are at an altitude of 3960 feet near the base of a mountain which has an altitude of 7214 feet, and in Colorado the ladybirds are at a height of 7160 feet at the top of a range that drops quickly, but not suddenly, to a flat plateau of 4994 feet; in both situations there is a difference of over 2000 feet between the level and the mountain-top.

## Air-currents and their Relation to Ladybirds found on Mountain-tops.

As the effect of air-currents upon the movements of ladybirds is fundamentally a physical and not a biological problem, I submitted certain queries to Dr. Shakespeare, Lecturer in Physics at Birmingham University, to whom I am indebted for much that follows.

The chief problems are, when biological forces have collected a large number of ladybirds together,

(1) What may happen to them if they fly into a current of air?

(2) How can a current of air deposit them on the top of a mountain?

We next need to know if and how much, ladybirds are helpless in a wind. It is certain that the ladybirds in the great gales that blow along the eastern side of the Rockies, and which are so strong that they can stop a high-powered car, would have no volition and would just go where they were carried.

At times winds have certainly blown ladybirds to destruction: for instance, there are a number of records of *C. septempunctata* being blown out to sea and drowned in enormous numbers, in

England, in late summer or early autumn, and Johnson (5) says, speaking of the conditions in the Western States, "These beetles (*Hippodamia*) are found in great numbers in the flotsam of the shore of large bodies of water when a certain sequence of winds occurs."

A flight of ladybirds might be caught by an air-current which was going up a mountain on its windward side. The air moves up the side of the mountain, curls over the top, twists down on the leeward side, and then, making a curl towards the earth, turns upwards towards the summit, so that the minimum speed would be on the leeward side, just below the top.

The minimum buoyancy will always be at the highest point.

If the wind up the side of the mountain is very gentle, there is no reason why the ladybird should not drop on to the ground whenever it so wished, but if the rate of the wind-movement was strong there must be a definite rate when the ladybird could not drop, its weight being so small in relation to the speed at which it was being carried along.

Any considerable change in altitude—say, from sea-level to 1000 feet, or from 3000 feet to 8000 feet—would cause the ladybird to drop owing to diminution of buoyancy. It is conceivable that a gale blowing ladybirds from the plateau at 5000 to the top of Horse Tooth at 7160 might so quickly reduce the buoyancy that they would be killed.

There are two principal factors involved—the rate of the wind and the rate of the reduction of the buoyancy.

The chance of the ladybird falling to the ground would be greatest when there is a combination of a minimum velocity and a minimum of buoyancy; this position will probably be just below the summit on the leeward side of the mountain. If they were deposited in this position by a wind, they would, owing to their undoubted tendency to go upwards, probably finally find their way to the top of the mountain.

The other factor to be considered is cold. Would the reduction of the temperature at the top of the mountain be sufficient to cause a sudden drop to the ground in that particular position? The reduction of temperature between the valley and the mountain-top is not sudden, but gradual, about ten degrees for every 3000 feet. If there is a minimum temperature at which ladybirds would automatically seek shelter, and that is, I think, sufficiently clear, even from my rough experiments in the Yosemite Valley, that temperature might be reached, and the ladybirds drop anywhere between the valley and the summit, and not necessarily at the top. The effect of cold alone would not, therefore, be expected to play a big part in making the ladybirds take up their position on the top of the mountains.

We do not yet know how far ladybirds can adapt themselves to rapidly changing altitudes, but we do know that man has considerable difficulty. As soon as material is available, experiments will be made to elucidate this point. It may be that

the ladybird that has grown to maturity at sea-level is quite incapable of living at an altitude of 8000 feet, and that, unless caught in a gale, it would automatically settle and hibernate at much lower altitudes.

## Summary.

1. Crude experiments in the Yosemite Valley show that *Hippodamia convergens* responds by movement to both light and heat stimuli, whether separate or combined. The optimum for each has yet to be determined.

2. The capacity to respond depends upon the length of time since hibernation began. A seasonal physiological insensitiveness to stimuli may be of considerable survival value.

3. *Hippodamia convergens* ate raisins, which they appeared to find by chance, and some continued to eat even when the low temperature had driven most to shelter.

4. *Hippodamia convergens* may be found hibernating in large masses at a variety of altitudes, but what determines that altitude is not yet known, or whether ladybirds which have grown in an altitude of, for example, 1000 feet would be physiologically capable of hibernating at an altitude of 7000 feet.

5. When biological forces have collected ladybirds in large numbers, then only, air-currents may have considerable effect upon their distribution and the positions where they ultimately hibernate.

6. Air-currents of great velocity might destroy ladybirds.

7. The effect of change of buoyancy upon ladybirds has yet to be determined.

My thanks are due to Professor Carlier for allowing me to do heat and light experiments in his laboratory at Birmingham University, and to Dr. Essig for the use of his photograph.

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## EXPLANATION OF THE PLATE.

Fig. 1. The Eastern side of the Rocky Mountains in Colorado. The foreground has an approximate elevation of 5000 feet, and the highest summit, Horse Tooth, where the ladybirds hibernated, is 8000 feet.

2. The end of the Yosemite Valley. In the foreground is the patch of leafless Azaleas where the ladybirds were hibernating. The foreground of the picture is 3960 feet altitude, and the high mountain to the right is 8852 feet. Beyond the Azaleas is a small field, then an apple orchard, where large numbers of *Hippodamia* had been found at one period in the summer, and close to orchard there are pine-trees.

3. A nearer view of Horse Tooth Mountain showing the bare rocks.

4. *Axion phagiatum* (Oliver) hibernating in a corn-cup of *Quercus lobata*: this shows a definite orientation of the body.
(Photograph kindly lent by Dr. Essig of Berkeley University.)

## 33. Worm Parasites of Rats in the Zoological Gardens.

By R. T. Leiper, M.D., D.Sc., F.R.S., F.Z.S., London School of Hygiene and Tropical Medicine.

[Read June 1, 1926.]

For many years systematic examinations have been made of the animals dying in the Zoological Gardens, and records been kept of the entozoa found. No search appears to have been made for entozoa in the vermin living in the Gardens, although the introduction of many exotic species of rodents might have suggested that the rats in the Gardens might have acquired an usually interesting fauna.

Through the co-operation of the Superintendent, Dr. G. M. Vevers, 14 brown rats were caught in the Society's Gardens during the past winter. The number of species of helminths was disappointingly small when compared with those listed by Balfour in his paper (1922) entitled "Observations on Wild Rats in England with an Account of their Ecto- and Endoparasites." Out of 430 brown rats, the following parasites were recorded by him:—

| | Per cent. |
|---|---|
| *Hymenolepis diminuta* | 28·4 |
| ,, *nana* | 26·1 |
| *Heligmosomum braziliense* | 8·6 |
| ,, *vexillatum* | 0·2 |
| *Viannaia* sp. ? | 0·7 |
| *Capillaria annulosa* | 0·4 |
| *Trichosomoides crassicauda* | 48·3 (out of 333). |
| *Cysticercus fasciolaris* | Common. |
| *Hepaticola hepatica* | Once. |

No flukes occurred, and the only tapeworm found by us in the 14 rats was a single specimen of *Hymenolepis diminuta*. No larval tapeworms occurred in the liver. In 5 out of the 14 rats, the liver showed serpenticular whitish streaks indicative of infection with *Capillaria hepatica*. In the bladder-wall *Trichosomoides crassicauda* was common. In the lumen of the gut two species occurred, viz., *Protospirura muris* adults in the stomach of one case and the macerated females of a form probably identical with *Heligmosomum braziliense* in the intestine of two cases. In 7 out of the 14 rats *Capillaria* were found in the mucosa of the œsophagus, stomach, and small intestine. In one rat immature adults of *Protospirura muris* were found in the stomach-wall and in the mesentery attached to the stomach and liver. These forms appear to be identical with those named by

Rudolphi *Filaria musculi*, for they correspond in position with the description given by Rudolphi, viz. "Hab. in abdomine *Muris musculi* circa ventriculum et hepar."

Recently Baylis and Daubney have given *Filaria musculi* Rud., 1819, as type of *Gongylonema* on the assumption that *Gongylonema minimum* Molin, 1857, is a synonym of *Filaria musculi*. In this they have followed Hall (1916), but the type of *Gongylonema* must be *Gongylonema minimum* Molin, 1857, or *Gongylonema* must replace *Protospirura* and *Myzomimus* Stiles, 1892, be restored for the genus which is now called *Gongylonema*.

The most important and interesting find in the Zoo rats was the roundworm, *Gongylonema neoplasticum*, which is now recorded from the British Isles for the first time. This species is common in South America and the West Indies, and has been found in Europe only in Denmark and Holland, in or near sugar factories at the large ports. The usual intermediate host is *Periplaneta americana*, which is brought to Europe in sugar cargoes. This cockroach seems to have been established in the Reptile House of the Zoological Gardens for several years, and has been used for class purposes by many teachers of zoology. It is surprising, therefore, that the larval stages of *Gongylonema neoplasticum* have not yet been recorded from these cockroaches by zoologists in this country, for out of 180 specimens collected from the Reptile House 143 were infested with the larvæ. It is evident that the infection of *Gongylonema* found in Zoo rats is derived from these cockroaches.

The genus *Gongylonema* contains a number of other species besides that found in the rat. These usually occur in ruminants, but none have been reported from the British Isles, and recent investigations in Scotland by Cameron (1923), and in England and Ireland by the collectors of the Institute of Agricultural Parasitology under my direction, have given entirely negative results.

During the last two or three years, the lay press has put prominently before the public the view that "Cancer Houses" are well-established realities, and the unequal geographical and topographical distribution of cancer in man in certain localities has been associated by Dr. Sambon with the presence of rats and cockroaches in these so-called "Cancer Houses." Dr. Sambon has assumed (1925, p. 65) that "the *Gongylonema*, known to be a cancer-producing agent in the rat, seems an equally likely factor in the incidence of cancer among human beings in certain regions such as the Romagna and the Trentino," where "the disease affects principally the upper portion of the alimentary tract." As acceptance of his views would imply that in the Zoological Gardens we had a potential source of public danger, it seems desirable to state grounds for believing these to be untenable.

From the published reports of investigations made in Italy by Dr. Sambon (1924–1925), Baylis, and other members of the British Museum Staff (1924 *a*, 1925 *b*, 1925 *c*) in the Italian

villages where cancer in man is so rife and where they carried out their investigations it is evident that

(*a*) *Gongylonema neoplasticum* does not occur there in the rat; it does not appear to have been recorded from Italy.
(*b*) The natural intermediate host, *Periplaneta americana*, does not occur, while *Blatta orientalis*, a possible alternative intermediary, is similarly absent from certain notorious cancer villages, *e. g.*, Villa Lagarina.
(*c*) No case of *Gongylonema neoplasticum* has yet been found in man in Italy or elsewhere.
(*d*) Cockroaches and other vermin collected from healthy and "cancer" houses have not been found infected with *Gongylonema* larvæ.
(*e*) Cancerous growths have never been found associated with any other species of the genus *Gongylonema*.

Sambon (1924) and Baylis (1925 *a*) found that sheep and cattle in the neighbourhood of the Italian villages where they made their investigations, were commonly infected with another species of *Gongylonema*, but they have failed to show any correlation between these field infestations and the peculiar limitation of cancer to certain houses or streets in the villages surrounded by these infected fields.

Baylis (1925 *b*) has succeeded in showing that the case of *Gongylonema* recorded by Alessandrini in a young woman, was due to infection with the same species as that found in the Pig, viz., *Gongylonema pulchrum*. It is significant, however, that in the recent publication by Baylis, Pan and J. Sambon, there is no mention of the presence of *G. pulchrum* in pigs in the villages of the Trentino. Baylis (1925 *c*) has published, however, a review of the species of the genus *Gongylonema* in which he holds that the forms found in sheep and cattle, and hitherto named *G. scutatum*, are identical with, or merely host variations of, *G. pulchrum* of pigs, and he merges *G. scutatum* in the synonymy of *G. pulchrum*. He also goes so far as to suggest that *G. neoplasticum* may be similarly merged, the differences in size and in certain measurements being possibly due to host influence. The subject is one which, as he says, can only be determined by experiment. It is, however, germane to the present discussion, for the hypothesis that *Gongylonema scutatum* of sheep and cattle, *Gongylonema pulchrum* of pigs, and *Gongylonema neoplasticum* of rats are identical and interchangeable forms, might now be used in support of Dr. Sambon's views, although it would be difficult to find adequate reason for assuming, in lieu of evidence, that rats infected in the fields with *Gongylonema* from farm animals by eating dung-beetles, should return inevitably to those houses or streets where cancer cases had previously occurred. Moreover, there is the difficulty of finding among the vermin of "cancer-houses" say, in the village of Villa Lagarina (*vide* Baylis, Pan and J. Sambon, 1925), a suitable

intermediate host which would convey the infection, if it were eaten uncooked by man.

The material obtained from the cockroaches in the Zoological Gardens has enabled us to solve by experiment the question of the variability of the characters of *Gongylonema* in the rat. Infected specimens of *Periplaneta americana* were divided longitudinally. One half was fed to laboratory-bred rats, the other to lambs bred on the Experimental Farm of the Institute of Agricultural Parasitology at St. Albans. Two series of experiments were carried out. From the first, 17 adult *Gongylonema* were recovered from the rat and one from the sheep. In the second, four adult *Gongylonema* were found in the rats, and four in the sheep. The male worms from both kinds of hosts were practically identical, as shown by the measurements given in the accompanying table. Moreover, they corresponded very closely with the measurements obtained from adult *Gongylonema neoplasticum* found in the Zoo rats and with those given by Baylis (1925 *a*) for *G. neoplasticum*. These results are positive and conclusive. They show that although *Gongylonema neoplasticum* can under experimental conditions be developed in sheep, in that abnormal host it retains the morphology which is characteristic of it in its normal host, the rat.

| | *Gongylonema neoplasticum.* | | | | | | | *G. scutatum.* |
|---|---|---|---|---|---|---|---|---|
| | Baylis. | Experimental Infections by Leiper. | | | | | | Baylis. |
| | | Sheep. | | Rats. | | | | |
| | | A. | B. | C. | D. | E. | F. | |
| | mm. | mm. | | mm. | | | | mm. |
| Total length of adult male .... | 7·4–11·1 | 6·75 | 7·2 | 8·8 | 8·42 | 8·89 | 11·05 | 30–62 |
| Length of right spicule ......... | 0·1–0·112 | 0·09 | 0·09 | 0·09 | 0·1 | 0·09 | 0·09 | 0·12–0·18 |
| Length of left spicule ......... | 0·59–0·67 | 0·52 | 0·49 | 0·54 | 0·64 | 0·56 | 0·76 | 5·0–23·0 |

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**Baylis**, H. A., & **Daubney**, R. 1926. "A Synopsis of the Families and Genera of Nematoda," p. 216.

## 34. Gapes. By R. T. Leiper, M.D., D.Sc., F.R.S., F.Z.S. (Professor of Helminthology in the University of London, London School of Hygiene and Tropical Medicine).

[Read June 1, 1926.]

One of the most important causes of losses in the poultry industry is the Gape-worm (*Syngamus trachealis*), which causes a heavy mortality every spring in young chickens. Those which survive are dwarfed and of poor physique.

Several years ago Dr. Chalmers Mitchell, Secretary of the Society, drew my attention to the need of renewed investigations to clear up many important points in the life-history and mode of spread of this parasite. Although I was unable to undertake the proposed enquiry at that time, I always kept his suggestion in mind and was able a few years ago and more recently to provide opportunities to some of my colleagues in the Institute of Agricultural Parasitology to take up the problem. Two years ago Dr. Ortlepp published the results of his study of the various stages in growth of the parasite from egg to adult. This work was carried out under conditions which excluded the intervention of any intermediate hosts. He showed that the complete cycle took place within one month and that the earth-worm, if it played any part, as suggested by Walker, was unessential. In America Ransom had shown that the Turkey when full grown was an important carrier of the Gape-worm, and he maintained that the Turkeys enabled the parasite to bridge a period from one spring to another, for the adult Hens were never found to harbour the parasites. According to his view, gapes was rife in chickens wherever turkeys were also kept on farms, and the abolition of the turkey would bring about an extermination of the disease in chickens. This view has been strongly supported in this country by Shipley and others. It does not, however, meet the whole situation here, for there are many authentic cases where gapes has suddenly appeared on poultry farms where turkeys have not been kept. Important light has recently been thrown on this mystery by E. A. Lewis, who, in the course of an examination of wild birds, found that no less than 35 per cent. of 482 starlings killed during the months November to February during the past winter were infected with gape-worm, and he has maintained, in a paper just published in the May number of the 'Journal of Helminthology,' that the migration of starlings plays a very important part in the spread of gapes. Lewis's figures were based on starlings shot around Aberystwyth; near St. Albans, about Easter time, 18 starlings were examined, of which 4 (*i.e.*, 22 per cent.) were infected.

The gape-worm of the starling, however, has been described as a distinct species by Schlotthauber and named *Syngamus pugionatus*. It seemed necessary, therefore, to determine experimentally if infective eggs derived from the starling could produce gapes in chickens. This has recently been done by us under carefully controlled conditions, and heavy infections have resulted. There seems no doubt, therefore, that the starling is probably an important and hitherto overlooked factor in the distribution of gapes. It is not the only one, however, for the turkey in this country is also a carrier of the gape-worm, and, as Dr. Ortlepp showed, infective eggs from the turkey can produce the disease in chickens. Of 70 turkeys killed for Christmas at farms around St. Albans 11 (*i.e.*, 15 per cent.) harboured gape-worms. In the turkey and in the starling only one or two worms are usually found under natural conditions. The adult pheasant is also known to harbour gape-worms, and one which died recently on Winches Farm was found infected.

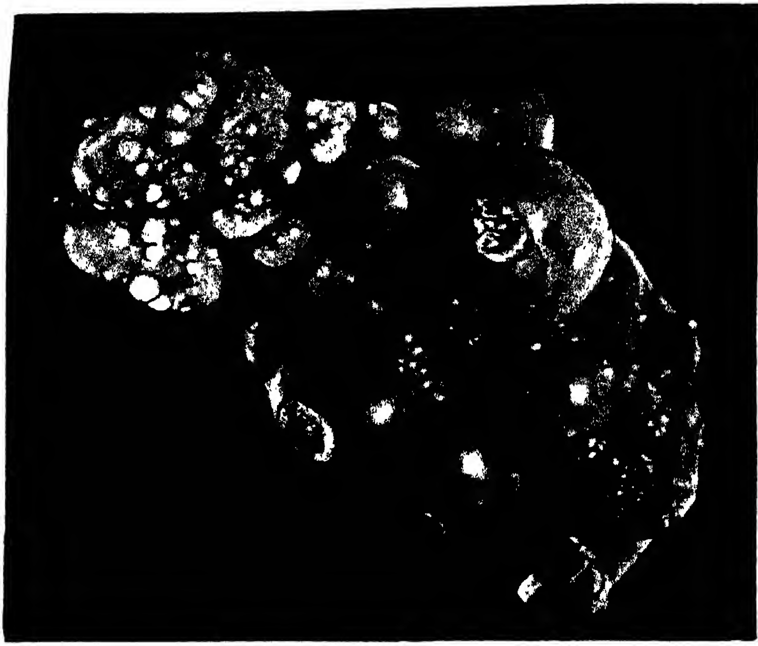

Fig. 1

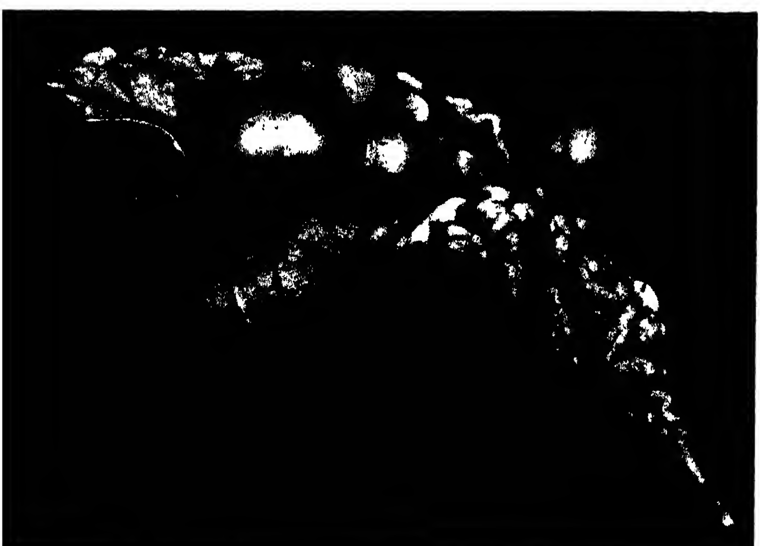

Fig. 2

Fig. 1. Ovary *Ornithorhynchus*. Stage 1.
Fig. 2. Ovary *Echidna*. Stage 6.


Fig. 3


Fig. 4

Fig. 3. Wall of follicle.
Fig. 4. Medullary region, ovary. *Ornithorhynchus*.

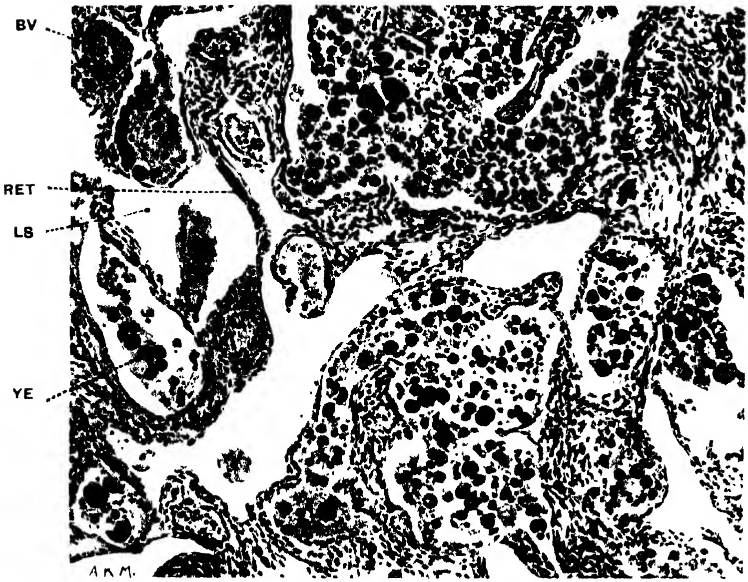


Fig. 5

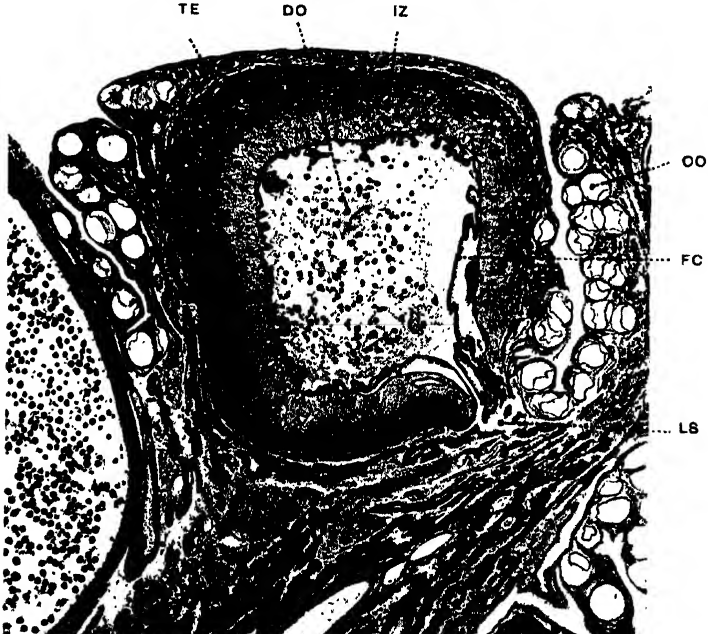


Fig. 6

Fig. 5. Medullary region, ovary.
Fig. 6. Atretic follicle. *Ornithorhynchus.*

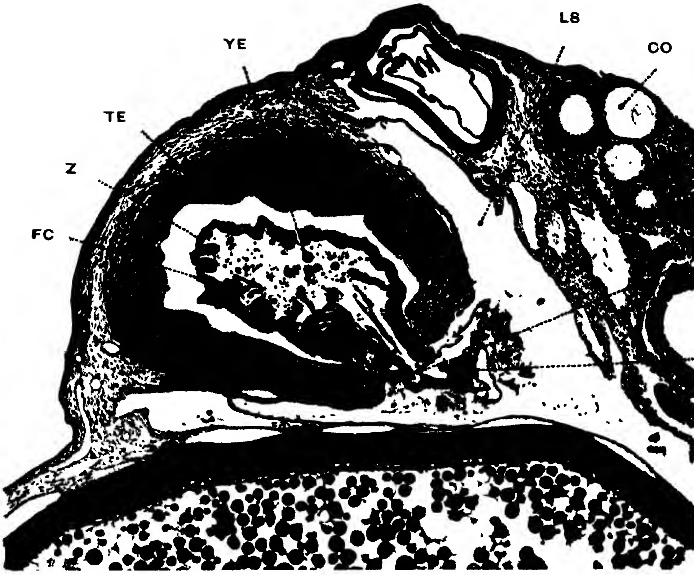


Fig. 7.

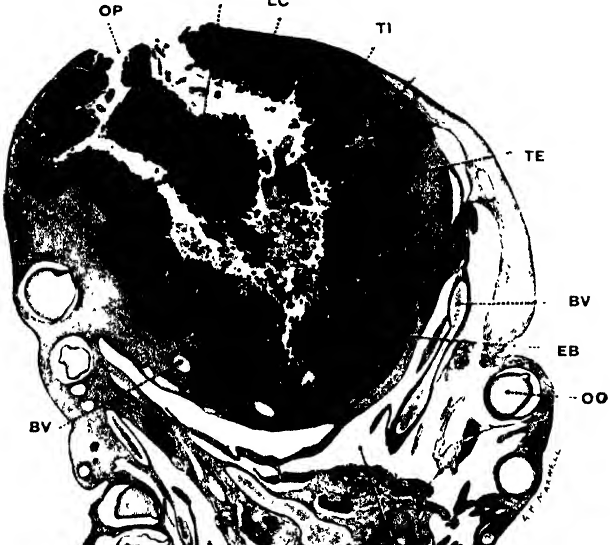


Fig. 8

Fig. 7. Atretic follicle.
Fig. 8. Corpus luteum, Stage 1a, *Ornithorhynchus*.

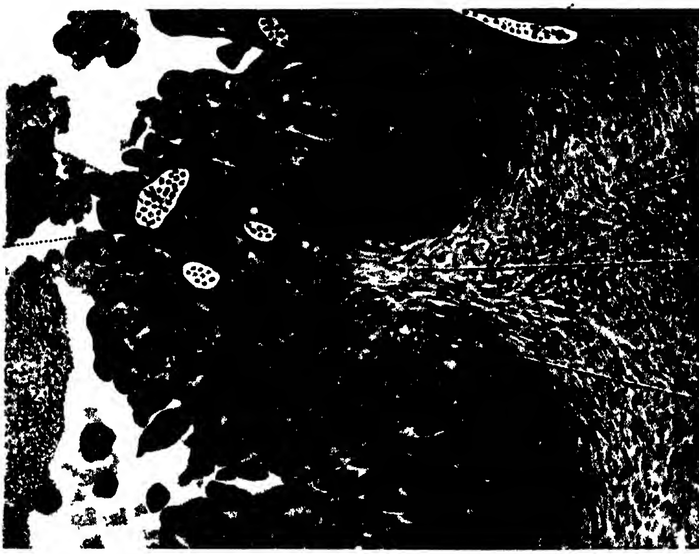


Fig. 9.

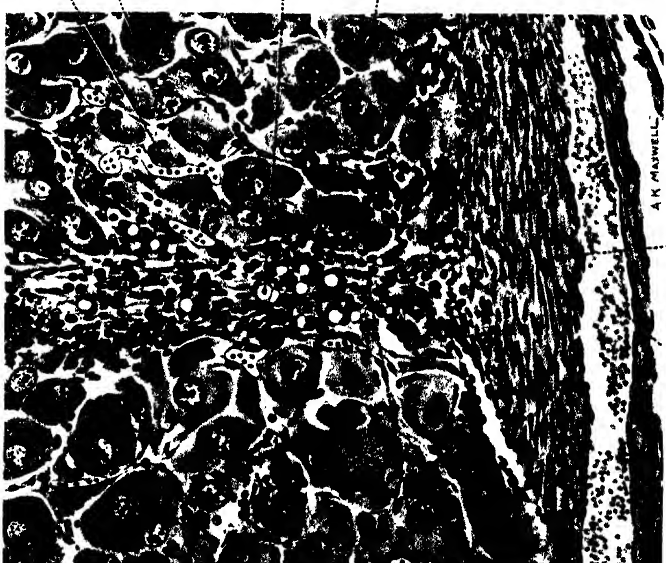


Fig. 10.

Fig 9. Corpus luteum, Stage IA.
Fig. 10. Corpus luteum, Stage II.

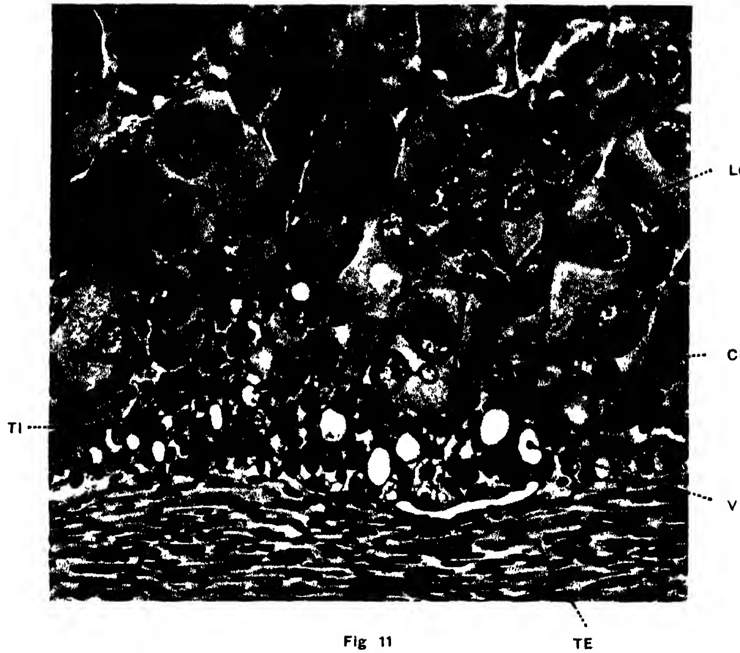


Fig 11

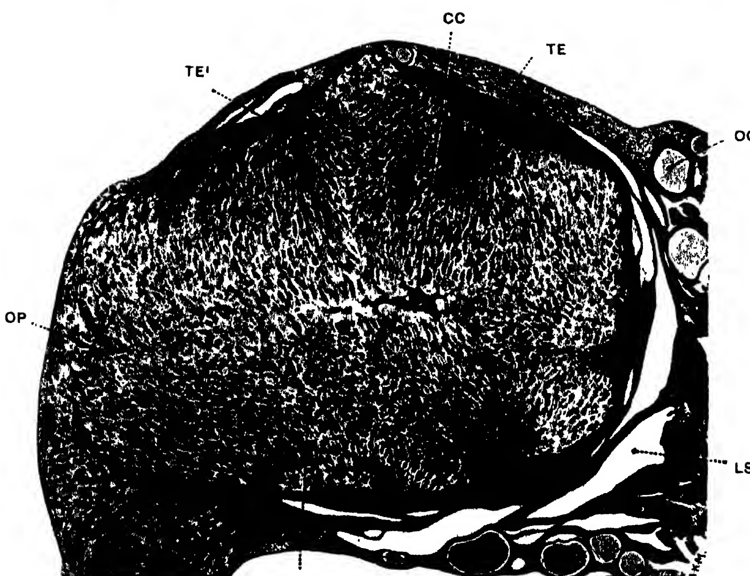


Fig. 12

Fig. 11. Corpus luteum, Stage II.
Fig. 12. Corpus luteum, Stage III.

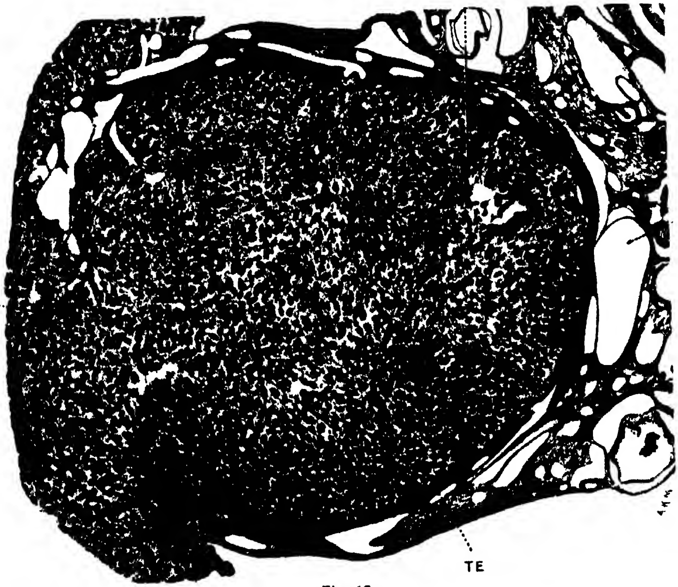


Fig 13

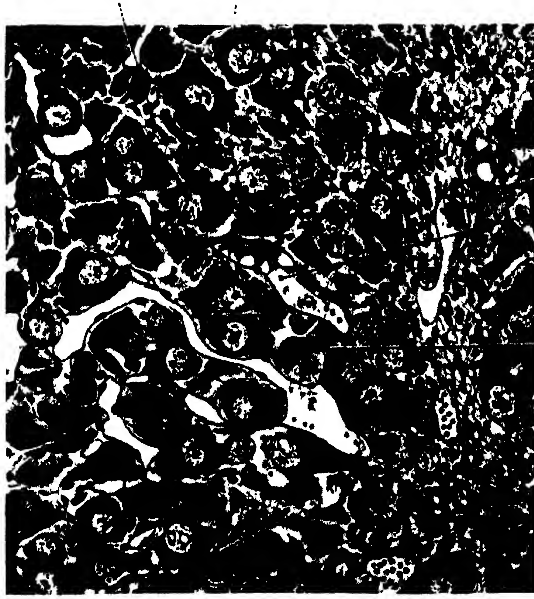


Fig. 14

Figs. 13, 14. Corpus luteum, Stage IV.

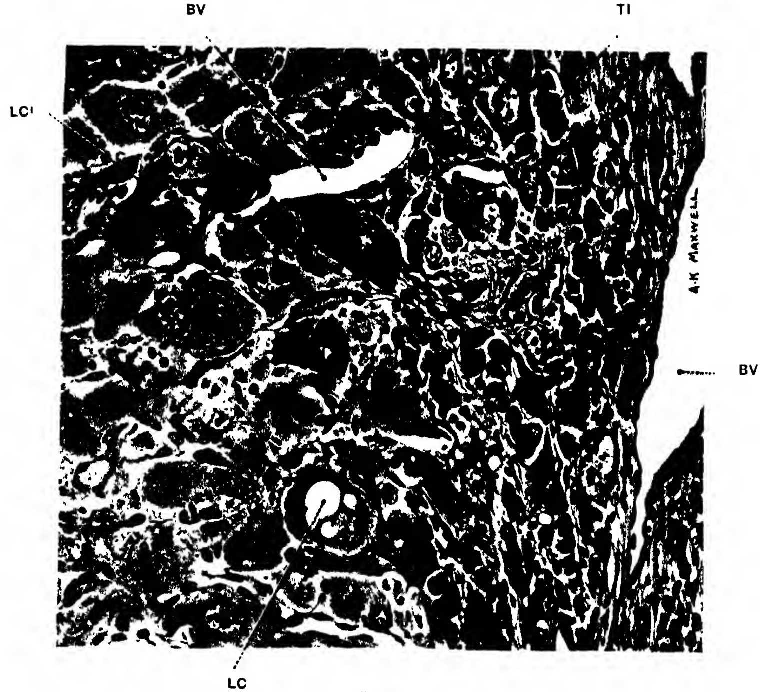


Fig. 15

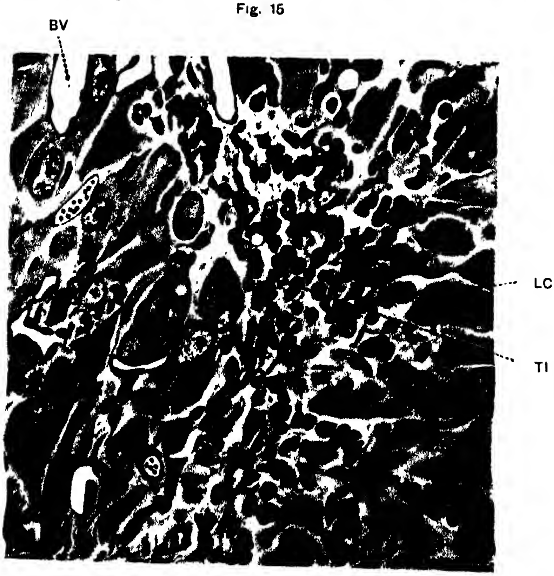


Fig. 16

Figs. 15, 16. Corpus luteum, Stage V.

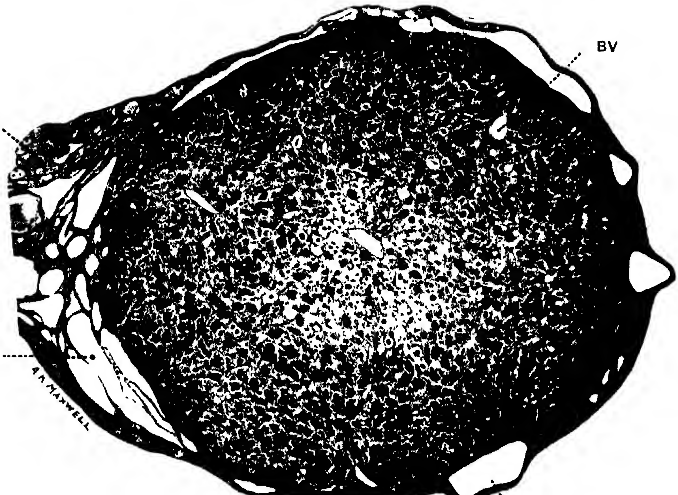


Fig 17


Fig. 18

Figs. 17, 18 Corpus luteum, *Echidna*, Stage VI.


Fig. 19. Corpus luteum, *Echidna*, Stage VI.

# 35. The Corpus Luteum of the Monotremata.

By Professor J. P. Hill, F.R.S., F.Z.S., University College, London, and Professor J. Brontë Gatenby, D.Sc. (Lond.), D.Phil. (Oxon.), Trinity College, Dublin.

[Received June 1, 1926: Read June 15, 1926.]

(Plates I.-X.; Text-figures 1–11.)

(From the Department of Embryology, Institute of Anatomy, University College, London.)

Contents.



## Introduction.

In this paper we have given an account of the formation and structure of the corpus luteum in *Ornithorhynchus*, supplemented by some observations on that of *Echidna*. The corpus luteum of the Monotremes proves to be a remarkably well-developed glandular organ, essentially similar to that of the higher Mammals but presenting peculiarities of its own and of considerable interest from the point of view of its histogenesis and its minute structure, and in its bearings on the question of the functions of the corpus luteum in the Mammals generally. We are able to demonstrate that the luteal cells which reach a relatively large size, and are, unmistakeably, functionally active elements, are derived exclusively from the cells of the follicular epithelium; and we are also able to show that the cells of the theca interna, which remain distinct from the luteal cells, participate with the fibrous theca externa in the formation of the organ. We have given some account of the minute structure of the luteal

cells and of the changes in their nuclei, but owing to the lack of suitably fixed preparations we have not been able to discuss as fully as we should have liked the history of the cytoplasmic organs (Golgi-bodies and mitochondria) and their relations to the secretory products which are elaborated, as in the higher Mammals by the luteal and theca-interna cells.

The material of *Platypus*, though not very extensive, is adequate for the main purpose in view, and was fixed in a variety of fluids (Picro-nitric Acid, Picro-nitro-osmic Acid, Zenker's and Flemming's Fluids, Formalin), and for general purposes is on the whole well preserved. Most of it was obtained in Australia by one of us (J.P.H.) in the years 1896–1905 with the aid of grants from the Government Grant Committee of the Royal Society, and comprises the ovaries of females, shot in the months of August and September, with the object of obtaining the intra-uterine stages of development of the eggs, some of which have been described by Wilson and Hill in their paper on the development of *Ornithorhynchus* (**43**).

No systematic attempt was ever made to obtain females after laying, and consequently we have no authenticated material from brooding and lactating females of *Platypus*, and are unable to give any account of the later history of the corpus luteum in this species. We possess, however, the ovary of an Echidna killed shortly after the laying of the egg (our stage VI) which has proved of value, since it has enabled us to demonstrate that the corpus luteum, at the time of the laying of the egg, is in active regression.

No attempt is made in this paper to correlate the stages in the formation of the corpus luteum with the structural changes in the uterine portion of the oviduct and in the mammary glands. Our material of the latter is, unfortunately, somewhat fragmentary, but a description, by Miss C. J. Hill, of the uterine changes during pregnancy is nearing completion.

The staining of some of the serial sections we have used in this work was carried out some years ago by Dr. (now Professor) C. H. O'Donoghue, with a view to collaboration with one of us, but circumstances prevented the carrying out of that plan.

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Our existing knowledge of the corpus luteum in the Monotremes is extremely scanty. Various authors, Sandes (**37**), O'Donoghue (**33**), Marshall (**27**), have testified to its existence, in view of the opinion of Born (expressed by Fraenkel & Cohn, **13**) and others that a corpus luteum was rudimentary or absent in the Monotremes as well as in the Marsupials. But the existence of a corpus luteum in the Monotremes could readily have been inferred from the description of Owen, published in 1834, and was definitely established by Caldwell in 1887.

In 1834, Owen (**34**) described and figured (pl. xxv. fig. 2) the corpora lutea in the left ovary of an Ornithorhynchus with two ova, three lines in diameter, in the corresponding uterus.

He writes (p. 559):—"The discharged ovisacs [corpora lutea] were of an elongated flask-shaped form, about three lines in length and two in diameter, with the margin of the orifice, through which the ovum and granular substance had passed, everted with a slight contraction, resembling the neck of a flask below the aperture. On compressing these ovisacs, small portions of coagulated material escaped. When longitudinally divided, they were found to consist of the same parts as the ovisac before impregnation, with the exception of the granular contents and granular stratum; but the theca, or innermost parietes of the sac, was much thickened, and encroached irregularly upon the empty space, so as to leave only a cylindrical passage to the external opening." This description of the macroscopic appearance of the early corpus luteum is singularly exact and is directly applicable to the conditions obtaining in the corpora lutea of our Stage I, except for the fact that the "granular stratum" (presumably the follicular epithelium) still persists as the lining of the ovisac.

Caldwell (7) in 1887, in his paper on the embryology of the Monotremata and Marsupialia, makes brief mention of the mode of formation of the corpus luteum in the Monotreme (p. 472). He states that, when the egg is received into the Fallopian tube, "a few cells of the follicular epithelium remain attached to the pro-albumen. The majority of the follicular cells remain behind, inside the follicle, and there they multiply so rapidly that very soon the whole cavity of the follicle is occupied by gigantic cells derived from continued division of the follicular epithelium, between which connective tissue cells have also grown in from the walls of the follicle itself." As stated in the sequel, we have not been able to observe any mitotic divisions in the follicular cells in our material. If such divisions do actually occur, we think they must be limited to an extremely short period, contemporaneous with, and just following ovulation. Apart from this, we fully confirm Caldwell's statements as to the origin of the luteal cells from the follicular epithelium and as to the presence of connective-tissue ingrowths from the thecal wall of the follicle.

We may add, however, that we have never been able to observe, round the ripe ovarian ovum in our Ornithorhynchus material, the layer of "pro-albumen" which he figures for Echidna (his pl. xxix. fig. 4) and describes as "a dense homogeneous substance," secreted by the follicular epithelium on its inner face, next the vitelline membrane.

Marshall, who examined some of our slides of corpus luteum, states, in a footnote to p. 143 of his book on "the Physiology of Reproduction," that "these sections show much hypertrophied and apparently fully developed luteal cells, but no trace of any ingrowth from the connective tissue wall of the corpus luteum." This latter statement is due to an oversight since in suitable sections such ingrowths are readily seen.

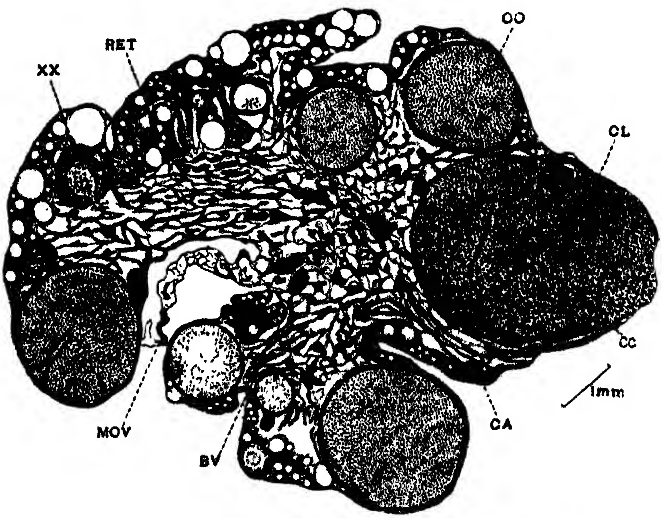
Blair Bell in his book on "the Sex-Complex" (5) illustrates in his fig. 4 a section of the ovary of *Ornithorhynchus* showing what

purports to be a corpus luteum and in his fig. 5 a section showing a corpus fibrosum. Fig. 4 is certainly none other than an atretic follicle, showing the much thickened theca externa and the theca interna also thickened, and enclosing a central cavity occupied by the degenerate remains of the ovum and its follicular epithelium.

## A.—The Ovary.

Whilst in *Platypus* the left ovary is alone functional, in *Echidna* we find that it is sometimes the left, sometimes the right which is functional.

Text-figure 1.




Low-power view of section of ovary of *Platypus* (Stage II) showing corpus luteum (*CL*) and oocytes (*OO*) in process of growth. *CA*. Cortical zone with young oocytes. *CC*. Remains of connective-tissue core of corpus luteum. *BV*. Blood-vessels. *MOV*. Mesovarium. *RET*. Medullary zone with connective-tissue trabeculæ and lymph-sinuses. *XX*. Atretic follicle.

The general structure of the ovary in *Platypus* has already been briefly described by one of us (Gatenby, 14). It may be recalled that it resembles that of the Sauropsida in appearance owing to the fact that the oocytes as they grow in size come to form marked spherical projections on its surface (Pl. I. figs. 1 & 2).

The oocytes, large and small (text-fig. 1, *OO*), are confined to a remarkably narrow cortical zone (*CA*) more or less folded and dense in character, whilst the main bulk of the ovary is formed by the central or medullary region (*RET*). This presents a very characteristic spongy or cavernous texture owing to the fact that it consists of a network of trabeculæ carrying the blood-vessels,

whilst the meshes are occupied by large lymph-channels or sinuses (text-fig. 1, and Pl. II. fig. 4, *LS*).

Two oocytes usually attain their full size at the same time, two being the usual number of eggs laid by the Platypus at one sitting; they are generally situated in fairly close proximity and form hemispherical projections from the surface of the ovary, with a diameter of 4·75 mm. or thereabouts. In the Monotremes, as is well known, no fluid-filled Graafian follicle is ever developed, the yolk-laden telolecithal oocyte measuring 4–4·5 mm. in diameter, occupying the whole of the space enclosed by the follicular wall.

The oocyte is invested by the zona (vitelline membrane of Caldwell), which at the stage of the full-grown oocyte has become extremely thin, and outside that is the follicular wall consisting from within outwards of the following layers: (*a*) the follicular epithelium, (*b*) the membrana propria, (*c*) the theca interna, (*d*) the theca externa.

### *Structure of the Follicular Wall.*

(a) *Follicular epithelium.* (Text-fig. 2, and Pl. II. fig. 3, *FC*.)

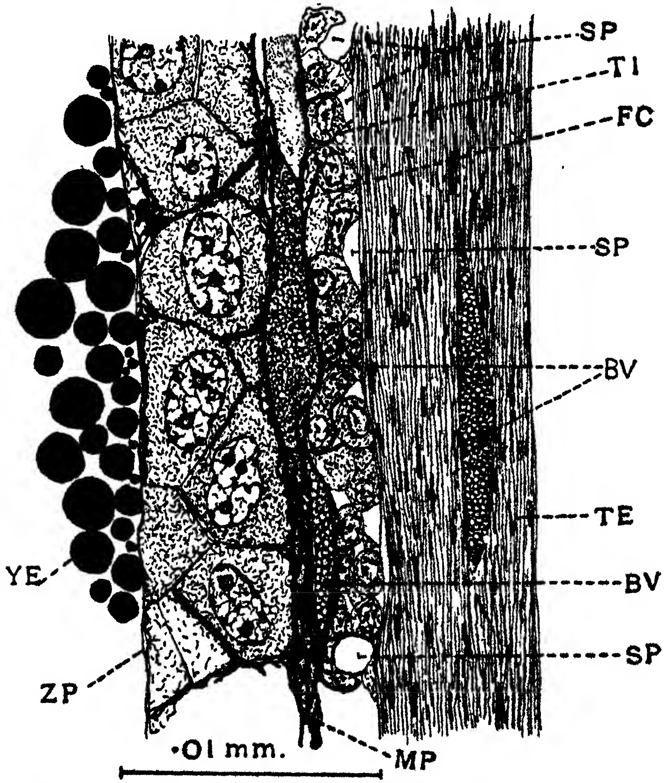
The follicular epithelium of the full-grown oocyte is formed of plump, glandular-looking cells of varied size and form (oblong, cubical or polygonal), arranged somewhat irregularly so as to form a layer about two cells thick, though here and there a single cell may extend through the entire thickness of the layer.

A somewhat remarkable feature of this layer is the presence of well-marked cuticular-looking membranes which enclose and delimit the cell-bodies, and which on the one hand unite to form a thin layer on the outer surface of the zona, and on the other pass into apparent continuity with the membrana propria either directly or by way of delicate fibrils crossing an irregular series of vacuolar spaces situated between the membrana propria and the membrane limiting the outer surfaces of the follicular cells. These apparent cell-membranes stain similarly to the membrana propria, and the relations suggest that they are of connective-tissue origin, though in that case we find it difficult to understand how they originate.

The nuclei of the follicular cells are large, darkly staining and ovoidal in form, their long axes tending to lie tangentially to the surface of the egg. They exhibit a characteristic structure (Pl. II. fig 3, and text-figs. 2 & 8 A). The nuclear reticulum is well marked and deeply staining, with small chromatic granules, especially distinct below the nuclear membrane. In the reticulum are situated a number of spherical nucleoli (three to six or more) presenting a characteristic ring-like appearance owing to the fact that their peripheral zone is markedly basophil, whilst their central region is chromophobe. They thus appear after staining with iron hæmatoxylin as minute black rings with a light centre. Around these nucleoli, the reticulum tends to be thickened, some-

times to such an extent, especially where two or more of them lie in proximity, as to produce the appearance of an irregular karyosome. Exceptionally there may be present, along with these ring-like nucleoli, a single large clear plasmosome like that characteristic of the nucleus of the luteal cell.

Text-figure 2.




High-power view of follicular wall of full-grown follicle (*Platypus*, III, *a*, 19.vii.01). The oocyte is on the left, *YE.* its yolk-spheres, *ZP.* zona. *FC.* Follicular epithelium. *MP.* Membrana propria. *TI.* Theca interna with spaces *SP.* *TE.* Theca externa. *BV.* Capillaries.

The follicular epithelium of the full-grown oocyte has a thickness of from ·022 to ·028 mm. The cells average in diameter about ·022 × ·015 mm. and their nuclei ·0169 × ·0097 mm.

As originally described by Caldwell (7) and more recently by Gatenby (14), the young oocyte is enclosed by a single-layered epithelium. It is still single layered round the 2–3 mm. oocyte (text-figs. 3–5, *FC*); the cells are small, brick-shaped or

cubical to flattened, and frequently appear isolated owing to the occurrence of curious gaps between them. Later, the cells divide, increase in size, and take on the irregular 2-rowed arrangement characteristic of the epithelium of the full-grown oocyte.

We venture to emphasize the fact, which is perhaps not devoid of physiological significance, that the follicular epithelium remains during the growth stages of the oocyte, a relatively thin inconspicuous layer and that it is only when the oocyte is completing its growth that it enlarges and along with the theca-interna cells takes on distinctly glandular characters.

(b) *Membrana propria.* (Pl. II. fig. 3, and text-fig 2, *MP.*)

Two views are held as to the nature of the so-called membrana propria, situated between the follicular epithelium and the theca interna, (*a*) that it represents the thickened basement membrane of the follicular epithelium, (*b*) that it is a derivative of the thecal connective-tissue investment.

In *Platypus* it varies greatly both in thickness and in appearance in different parts of its extent. It consists of a homogeneous matrix staining lightly with hæmatoxylin, which appears distinctly fenestrated especially on its side next the theca interna. In its substance, as well as on its surface, occur numbers of small flattened nuclei, which we interpret as the nuclei of its formative fibroblasts. Fine capillaries actually lie imbedded in the matrix of the membrane, though sometimes they are situated between it and the follicular epithelium. We consider that the membrana propria here is unquestionably of the nature of a fenestrated connective-tissue membrane, its formative fibroblasts being probably those which occur in the theca interna of the early oocyte (see below, p. 723, and text-figs. 3 & 5, *MPF*).

(c) *Theca interna.* (Pl. II. fig. 3, *TI*, and text-fig. 2.)

Outside the membrana propria, between that and the theca externa, is a discontinuous layer of small cells forming the theca interna. Quite absent in places, it varies from one to five cells in thickness. At its maximum, it is nearly as thick as the follicular epithelium. Apart from the capillaries that run in and through it in fair numbers, it consists of cells which we shall speak of as the theca-interna cells; no fibres are present or at all events are recognisable in our preparations, though it should be mentioned that prolongations from the collagenous material of the basement membrane pass into continuity with the cell-membranes and may perhaps form them. The cells are much smaller than those of the follicular epithelium, and are ovoidal or brick-shaped in form. Though their bounding cell-membranes are usually distinct, it is sometimes difficult to define their limits. Their cytoplasm stains rather lightly and is coarsely alveolar in texture. Frequently it is definitely vacuolated, and then the

layer presents a loose, sponge-like appearance. The nuclei are ovoidal or spherical (·0068 × ·0048 mm. in average diameter), and possess a distinct reticulum and a well-marked karyosome, minute ring-like nucleoli are also present.

In the theca interna of the full-grown follicle we have never observed spindle-shaped cells or fibroblasts intermixed with the theca-interna cells.

Unfortunately, the lack of fully osmicated material prevents us from elucidating the significance of the vacuolisation of the theca-interna cells

In the Pig, Corner (**9**, p. 141) describes the theca interna as consisting of "three to five layers of large 'epithelioid' cells." He states that in Bouin-fixed material the theca cells present a honeycombed appearance owing to the presence of vacuoles, "due, at least in part, to the presence in the fresh tissue of granules of a fat-like substance packed closely into the theca cells." From its reactions, he assumes that it is "of lipoid nature but is perhaps not a neutral fat." In addition, he states that many of the theca cells contain, instead of lipoid granules, vacuoles filled by a material which is not rendered insoluble by combination with osmic acid.

In the Rat, Long & Evans (**24**, p. 38) state that "in the ripe Graafian follicle just preceding rupture one may observe that the cells of the theca interna are well laden with fair-sized lipoid spherules which blacken readily with osmic acid."

(d) *Theca externa.* (Pl. II. fig. 3, and text-fig. 2, *TE.*)

At the stage of the full-grown oocyte, the theca interna is clearly marked off from the outer layer of the follicular wall, the theca externa. This consists of a well-marked layer of white fibrous connective tissue, the nuclei of its related fibroblasts appearing as elongated flattened structures, situated between the fibre-bundles. In the Pig, Corner (**9**) states that smooth muscle-fibres are present in the theca externa, but they are absent in *Platypus*. Further, preparations specially stained for elastic fibres failed to yield definite evidence of their presence, though the elastic fibres in the arterial walls were specifically stained. It would therefore appear that white or collagen fibres are alone present in the theca externa in *Platypus*.

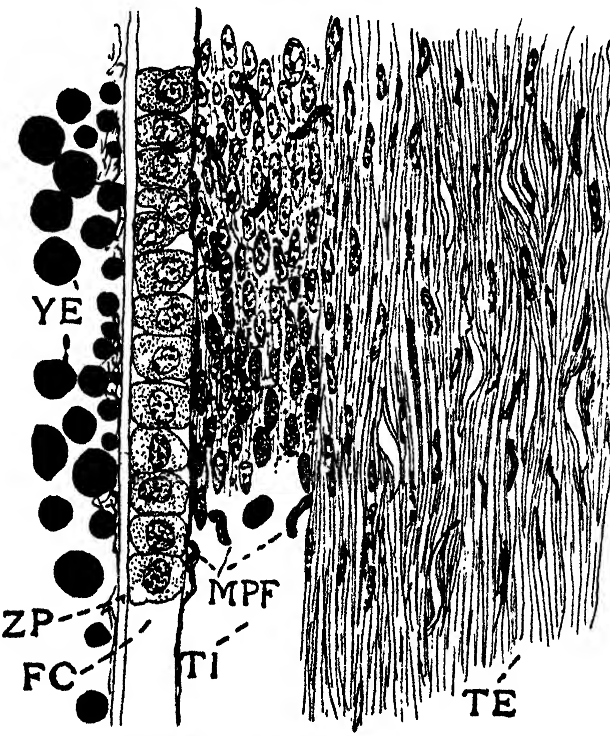
### *Origin of the Theca interna.*

In view of the subsequent history of the theca-interna cells, we have endeavoured to determine their origin. The early oocytes up to a diameter of about ·5 mm. are surrounded, externally to the follicular epithelium, by a thin thecal coat composed of concentrically-arranged small flattened cells derived from the ovarian stroma. By the time the oocyte has attained a diameter of ·75 mm., the primary thecal investment, now thicker, is distinguishable in preparations stained by hæmatoxylin followed by

Pasini's stain into an inner purely cellular zone and an outer blue-staining fibrous zone.

In the 2 mm. oocyte (text-fig. 3) stained by the same technique, these two zones are perfectly distinct. The outer zone, the thicker of the two, represents the theca externa (*TE*), and consists of blue-stained fibre-bundles in between which are situated the spindle-shaped fibroblasts with red-stained nuclei.

Text-figure 3.




Follicular wall of oocyte, about 2 mm. in diameter.

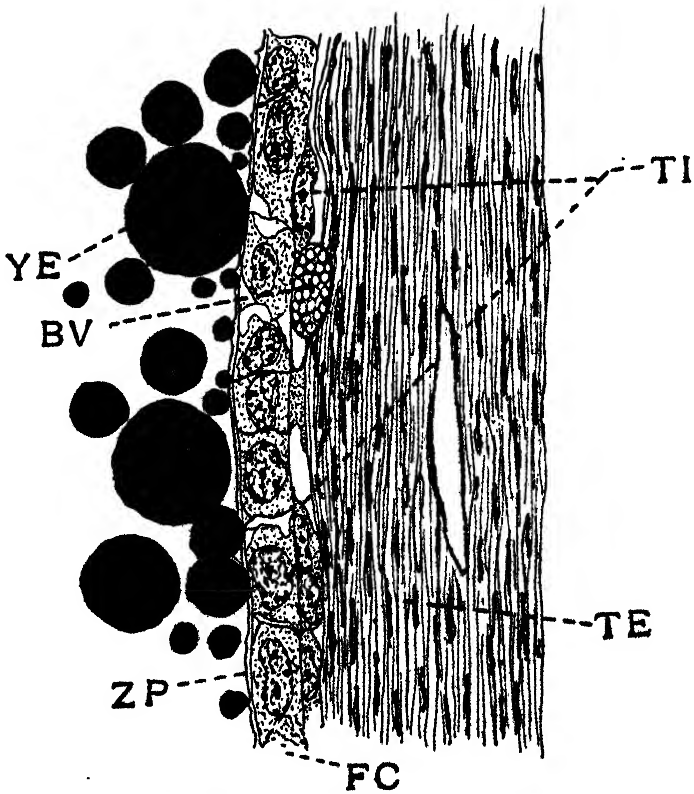
*FC*. Follicular epithelium. *TI*. Theca interna, with nuclei of fibroblasts (*MPF*). *TE*. Theca externa. *YE*. Yolk-spheres of oocyte. *ZP*. Zona.

The inner zone (theca interna, *TI*), stained of a reddish tint, is thinner than the outer and is purely cellular, consisting of several strata of small compactly-arranged cells, with flattened rod-like or oblong nuclei. In addition, there are present here and there, nuclei (*MPF*) which are of more elongated form and stain more deeply than the others. These, we think, are possibly the nuclei of the fibroblasts which are concerned in the formation

of the fenestrated membrana propria. Capillaries are already present in the theca interna (text-fig. 4, *BV*).

We conclude that the stroma-cells of the primitive theca give origin on the one hand to the cells of the theca interna and the fibroblasts of the membrana propria, and on the other to the fibroblasts of the theca externa. This conclusion is in agreement

Text-figure 4.




Follicular wall of oocyte, about 2·75 mm. in diameter.

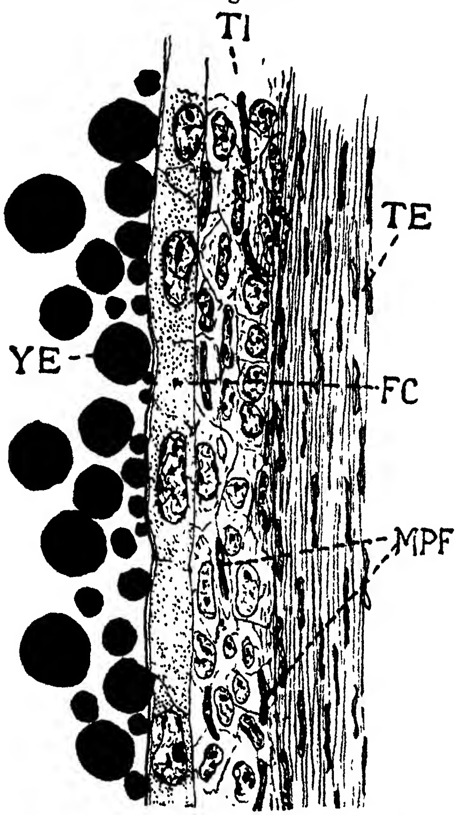
*BV*. Capillary in theca interna. *FC*. Follicular epithelium. *TI*. Theca interna. *TE*. Theca externa. *YE*. Yolk-spheres of oocyte. *ZP*. Zona.

with that of B. M. Allen (1) that in the Rabbit the theca externa and theca interna are both derived from the connective-tissue stroma of the ovary.

Already in the 2·75 mm. and the 3 mm. oocytes (text-figs. 4 & 5, *TI*) the theca-interna cells have commenced to enlarge, but they would seem to attain their definite characters only in

oocytes nearing the end of their growth-period. It should be understood that considerable differences in the degree of development of the theca interna are found in different follicles and even

Text-figure 5.




Follicular wall of oocyte, about 3 mm. in diameter.

*FC*. Follicular epithelium. *TI*. Theca interna with nuclei (*MPF*) of supposed fibroblasts of membrana propria. *TE*. Theca externa. *YE*. Yolk-spheres of oocyte. *ZP*. Zona.

in parts of the same follicle (*cf.* the thickness of this layer in the 2·75 mm. oocyte, text-fig. 4, with that of the 3 mm. oocyte, text-fig. 5).

*Medullary Region of Ovary.*

One of the most striking features of the *Platypus* ovary to which Gatenby has previously (14) directed attention, is the structure of the central or medullary region. This consists of

an irregular network of connective-tissue trabeculæ carrying numerous blood-vessels and enclosing numerous wide and correspondingly irregular cavities which are none other than enlarged lymph-channels of the nature of sinuses (text-fig. 1, and Pl. II. fig. 4, *LS*). They are lined by an endothelial layer, often of considerable thickness, and are provided here and there with valves. Frequently one finds the blood-vessels of the trabecular stroma more or less completely surrounded by such sinuses. They occur directly below the cortical zone, with the result that the follicles as they increase in size bulge into them, and so come to be surrounded except on their outer surfaces "in a basket-like area formed by connective-tissue trabeculæ and intervening lacunæ filled with liquid" (Gatenby, **14**), an arrangement which is obviously ideal from the point of view of the nutrition of the growing oocyte.

The contents of these lymph-sinuses are in many of our sections of a remarkable character. In the material previously studied by Gatenby no contents were noted in these sinuses, and it was stated that they "seem to be occupied by a non-corpuscular fluid," but, since examining a more extensive collection, we have been able to find examples where the sinuses contain extraordinarily large quantities of formed material. The condition of the ovaries in our collection varied from examples in which the sinuses were devoid of visible coagula to others in which a structureless oxyphil substance was present (Pl. II. fig. 4), and finally to examples where the sinuses contained a coagulum with large quantities of yolk-granules (Pl. III. fig. 5, *YE*), appearing mostly as irregular masses in varying stages of dissolution. Examination of such masses, especially in Pasini-stained preparations, reveals the fact that in many cases the yolk-spheres are actually intracellular, having been engulfed by phagocytic wandering cells. The entire process is worthy of detailed description, but need not detain us here. The presence of yolk-granules in these lymph-sinuses is to be explained as due to a peculiar process of follicular atresia referred to below, in which the oocyte for some unknown reason undergoes disintegration after the formation of the yolk-spheres, with subsequent rupture of the follicular wall and the release of the contents into the adjacent lymph-sinuses.

The medullary trabeculæ, in which are situated numerous blood-vessels, consist of a loose connective tissue, containing anastomosing bundles of collagen fibres and also bundles of smooth muscle-fibres. The connective tissue is very rich in cells, plasma cells being specially abundant, whilst aggregations of lymphoid cells are frequently met with.

It is worthy of note that we have failed to find in the ovary of *Platypus* any cells of the character of interstitial cells, though Gatenby (**14**) has recorded the existence of such in the testis.

As concerns the lymphatics of the ovary, the only other mammal we know of which approaches *Platypus* in the degree of their

development, is *Vesperugo noctula* where, according to O. van der Stricht (**44**), "les lymphatiques engendrent de vaste carrefours cloissonés, des loges volumineuses en communication les unes avec les autres par des ouvertures de diamètre variable" (p. 645). Van der Stricht believed that the lymphatic spaces and vessels absorb all the substances elaborated by the corpus luteum and transport them into the blood.

## *Follicular Atresia.*

Degeneration and resorption of ovarian ova (follicular atresia) are phenomena well known in the higher Mammals and also in the Reptiles and Birds (*cf.* Loyez (**25**), p. 193 & p. 266), but we know of no instance where the contents of the atretic follicles are directly discharged into the lymphatic system as is the case in *Ornithorhynchus*.

Follicular atresia is of common occurrence in the ovaries we have studied, and affects both small follicles with oocytes in which the yolk is not yet formed and larger follicles in the oocytes of which vitellogenesis is well advanced. In most cases after the breakdown of the ovum, the thecal investments hypertrophy and form a thick-walled sphere enclosing the folded and more or less altered follicular epithelium and the correspondingly folded and thickened zona, whilst the central cavity is occupied by the broken-down cytoplasm and the yolk-spheres, if such have been formed. In the small atretic follicles the degenerate contents are apparently resorbed *in situ*, but in the larger they would usually appear to be discharged directly through a break in the follicular wall, into an underlying lymph-sinus. Ultimately, the atretic follicles form spherical fibrous nodules in the cortical stroma of the ovary.

The bursting of the atretic follicles into the lymph-sinuses is an extraordinary and, so far as we are aware, a unique phenomenon. It is illustrated in our figs. 6 & 7 (Pls. III. & IV.). In both cases illustrated, it will be seen that the thickened follicular wall presents a defect or opening on its deep surface. The opening is bounded by a more or less definite lip which projects into the lymph-sinus underlying the follicle, and through it the contents of the follicle are in process of being discharged into the sinus.

In Pl. III. fig. 6, the greatly thickened thecal investment of the follicle is readily distinguishable into a more deeply staining and fibrous outer zone, and an inner more cellular zone, permeated by numbers of small capillaries. The outer zone represents the theca externa in whole or in part, whilst the inner zone may represent the greatly hypertrophied theca interna, but is more probably a recently formed derivative of the theca externa. The membrana propria is still largely intact, whilst the one-layered and somewhat degenerate follicular epithelium and the zona (thicker than normal) are thrown into irregular low folds and are prolonged through the opening into the lymph-sinus. The cavity of the

follicle is still largely occupied by the broken-down cytoplasm and the yolk-spheres of the ovum.

Fig. 7 (Pl. IV.) illustrates a later stage in follicular atresia. The thecal coat is thick, but two zones are here not readily distinguishable in it. The follicular epithelium (*FC*) is still recognisable; it has shrunken away from the theca and is folded and more or less altered. The zona (*Z*) is also markedly folded and thickened and, with remnants of the follicular epithelium, is seen to project through the opening of the follicle into the large and conspicuous lymph-sinus which underlies and partly surrounds the follicle. In this case, most of the contents of the follicle have been discharged into the lymph-sinus, a process which results in the engorgement of the medullary sinuses, as shown in Pl. III. fig. 5.

### B.—Corpus Luteum.

The general appearance of the ovary with early corpora lutea is well seen in the photograph of the ovary reproduced as Pl. I. fig. 1. This ovary (Stage I, C) measured 14 mm. in length × 8·5 mm. in breadth and showed two corpora lutea, measuring in diameter about 3·5 mm. It was accompanied by a single uterine egg, 6 mm. in diameter and in an early stage of cleavage (? 19 blastomeres). There are, however, two corpora lutea in the ovary, from which we conclude that one of the two eggs ovulated has been lost. The corpora lutea are projecting bodies situated in proximity in the mid-region of the ovary. The upper one in the figure shows the opening through which the oocyte escaped and which leads directly into the still persistent follicular cavity. It is bounded by an irregular lip, inside which are visible the folds of the lining of the developing corpus luteum. The lower one shows the corresponding opening bounded by a lip which is here quite definite and rim-like. In both cases, the lip is seen in the sections to be formed of enlarged follicular epithelial (luteal) cells. As we shall see later, this protruding lip of luteal cells corresponds to "le bouchon épithélial obturateur" of O. van der Stricht and to the "Pfropf" of German writers. Immediately to the right of the corpora lutea are two spherical projections produced by oocytes, less than half grown. Further to the right and also to the left of the figure, the characteristically corrugated surface of the ovary is well seen, with the smaller oocytes forming raised, rounded areas, distributed all over it. The two small white bodies projecting on the surface towards the left are probably atretic follicles.

The ovary of our Stage IV shows the appearance of the corpora lutea at a later stage. The ovary measured 11·5 × 10 mm. in diameter. The uterus contained two eggs about 16·5 × 15 mm. in diameter, with embryos at a stage just a little later than Wilson & Hill's specimen H (43). The corpora lutea present the same projecting, ovoidal (potato-like) appearance as in fig. 1, but they are now distinctly larger, the one measuring

4·5 mm. in height × 3·5 mm. in thickness, and the other, 5 × 3 mm. On the blunt free extremity of each, there is visible a definite depression in the position of the opening in the earlier corpus luteum, but the opening is no longer patent nor is there a cavity in the corpus luteum. Both have become obliterated by the enlargement of the luteal cells. The latter, however, still project to form a "bouchon" or "plug" at the original site of the opening, marked by the depression, and are here freely exposed.

Text-fig. 1 represents a low-power view of a section through the entire ovary of Stage II; the figure shows the relatively large size of the fully-formed corpus luteum (*CL*), the cortical zone of the ovary alone containing eggs (*CA*), and the characteristic cavernous structure of the medullary zone (*RET*). The structure marked *XX* is an atretic follicle, which has ruptured into an underlying lymph-sinus and is in process of discharging the degenerated remains of the oocyte into the same. Another such follicle is shown in the figure just below *XX*.

Finally in this connection we present the photograph of the right ovary of an Echidna, shown in Pl. I. fig. 2. This ovary (Stage VI of our material) was derived from a female Echidna which laid a single egg whilst in captivity. The egg was found a day or two after laying, when the female was killed.

The right ovary in this case was functional and measured, 17 mm. in length, 7 mm. in greatest breadth, and 6 mm. in thickness. It exhibits a characteristically folded, corrugated surface, projecting from which are three medium-sized spherical follicles, two of them, a larger and a smaller, in contact, the third projecting from the right margin. Immediately below the two follicles in contact is seen the single corpus luteum, freely projecting, somewhat pear-shaped in form, and with a pedunculated base of attachment. It measured 4·5 mm. in height and 3·5 mm. in thickness, and at its apical extremity exhibited a small circular patch or scar marking the point of closure.

*Table of Measurements of Corpus luteal Elements.*

| *Stage.* | *Luteal Tissue.* | *Luteal Cells.* | *Luteal Nuclei.* | *Theca-interna Nuclei.* |
|---|---|---|---|---|
| Full-grown oocyte. (*a*, 19. vii. 01.) | ...... | (Follic. epithelium) ·022 × ·015 mm. | ·0169 × ·0097 mm. | |
| I, A ............ | 2·6 × 1·97 mm. | ·026 × ·018 mm. | ·019 × ·012 mm. | ·008 × ·006 mm. |
| II............ ... | 3·9 × 2·75 mm. | ·054 × ·037 mm. | ·024 × ·019 mm. | ·0078 × ·0059 mm. |
| III ............ | 3·2 × 2·18 mm. | ·06 × ·037 mm. | ·027 × ·020 mm. | ·0076 × ·0057 mm. |
| IV ... ........ | 3·7 × 2·6 mm. | ·047 × ·035 mm. | ·025 × ·019 mm. | ·0064 × ·0054 mm. |
| V ............... | 3·6 × 2·34 mm. | ·047 × ·03 mm. | ·025 × ·017 mm. | ·0065 × ·005 mm. |

*Formation of Corpus luteum.*

### Stage I.

We have grouped together in our first stage four ovaries, in regard to three of which we possess records relating to the intra-uterine eggs:—

I, A. (No. 1. 19. viii. 01). Ovary with two corpora lutea. Two intra-uterine eggs, C & CC, diameter 6·75 mm. The ovum of C after removal of the shell membrane and albumen measured in the stained sections, 3·8 × 3·7 mm. in diameter; the ovum of CC measured in spirit about 4·5 mm. in diameter.

Ovum C has recently been described by Gatenby & Hill (**16**). It is unsegmented, and probably at the stage of fertilization. The 1st polar body is separated off and divided into two, the 2nd polar body is in process of separation.

The corpus luteum (including the theca and the central cavity) has a diameter in section of 2·75 × 2·28 mm.; the luteal tissue (including the central cavity) measures 2·6 × 1·97 mm. in diameter.

I, B. (JN. 23. viii. 01), with two intra-uterine eggs (A & AA) 5·5 mm. in diameter; ovum, 4 mm. The ova are in the 8-celled stage of cleavage (*cf.* Wilson & Hill, **43**). Of this ovary we possess only a very incomplete series of sections passing through the periphery of the corpus luteum.

I, C. (JJ. ix. 05). Ovary 14 × 8·5 mm. in diameter, with two corpora lutea with a diameter in spirit of about 3·6 mm. (Pl. I. fig. 1). The single intra-uterine egg accompanying the ovary measures 6 mm. and the ovum 4·5 mm. in diameter. The ovum is in an early stage of cleavage (? about twenty blastomeres). The corpus luteum (including theca and central cavity) measures 2·5 × 2·08 mm., and the luteal tissue (including central cavity) 2·4 × 1·5 mm. in diameter.

I, D. (XII). Ovary with two corpora lutea. No record available of the intra-uterine eggs.

Corpus luteum (including theca and central cavity) 2·85 × 2·75 mm., and luteal tissue (including central cavity) 2·6 × 1·8 mm. in diameter.

It will be observed that the developmental stages related to three of these ovaries range from the unsegmented egg, through an 8-celled cleavage stage to one with about 20 blastomeres. In three of them certainly and presumably also in the fourth (I, B) the opening through which the oocyte escaped is still patent and leads into the hollow interior of the developing corpus luteum.

Ovary (I, A) is not only the earliest but is the best preserved of the four, and so has been selected as the basis of the following description.

In fig. 8 (Pl. IV.) is shown a low-power view of a section of a corpus luteum of this ovary. At *OP* is the opening through

which the oocyte escaped, the somewhat ragged margins of the aperture being formed by the cellular lining of the follicle. Partially filling the opening is the outer projecting extremity of an irregular mass which largely occupies the central part of the follicular cavity. This mass consists of an extensive clot of extravasated blood, intermingled with which are numerous large cells, especially abundant in the inner half of the cavity, and occurring either isolated or in groups. These cells are identical in character with those forming the superficial layer of the follicular lining, and it is obvious from the sections that they are simply detached cells of that layer (Pl. V. fig. 9).

The lining of the follicle (Pl. V. fig. 9) is formed by an irregular folded layer varying in thickness from about ·2 mm. to about ·5 mm. and with a quite uneven surface. Closer examination shows that it consists of two layers of cells, superficial and deep. The superficial layer is composed of large, deeply staining cells forming an irregular epithelium varying in thickness from two or three to twelve or more cells. The deep layer, of very different aspect to the superficial, is composed of cells much smaller and more lightly staining than those of the latter. It follows the irregular wavy contour of the superficial layer, and consequently is also of very variable thickness; in parts of its extent, it is only a few cells thick, in others, especially opposite the inward projections of the theca externa, where the superficial layer also happens to be thin, it appears locally thickened and, extending towards the free surface, may attain a thickness of ·25 mm. or more. It appears to be in process of invading the superficial layer, and here and there the small cells have already penetrated between the bases of the more deeply situated superficial cells. This deep layer rests directly on the fibrous theca externa, a relatively thick layer, from the inner surface of which arise a number of ridge-like projections which extend for a short distance into the cellular lining and which are better marked in ovary I, D than in I, A (Pl. V. fig. 9, *TE*). Besides these conspicuous projections, which, no doubt, owe their origin in the first instance, to the general contraction and folding of the follicular walls which result from ovulation, closer examination shows that strands of fibroblasts are already growing into the cellular lining, more particularly from the surfaces of the first mentioned projections. The ingrowing fibroblasts are as yet largely confined to the small-celled tissue of the deep layer (theca interna), though some few of them have already penetrated between the large cells of the superficial layer.

Numbers of fair-sized vessels are present in the theca externa, branches of which pass into the cellular lining either by way of the thecal projections or directly, to form well-marked capillaries which have already made their appearance between the large cells of the superficial layer (fig. 9, *BV*). In addition, there are present in the theca externa in I, D and to a lesser extent in I, A, a number of localised blood extravasations (Pl. IV. fig. 8, *EB*).

No trace remains of the so-called membrana propria of the follicular wall, but apart from this, it is evident that the three layers of the wall of the intact follicle are still present in that of the ruptured follicle. The large cells of the superficial layer of the follicular lining, above mentioned, together with the free cells in the follicular cavity, represent, unquestionably, the follicular epithelial cells or their derivatives, somewhat hypertrophied and in process of transformation into luteal cells, whilst the smaller cells of the deep layer, also without question, are to be regarded as the derivatives of the theca-interna cells of the ripe follicle.

The intact full-grown follicle in *Platypus* measures about 4·75 mm. in diameter, whilst the recently ruptured follicle in I, A measures only 2·75 × 2·28 mm. It has thus suffered a marked contraction (a phenomenon well known in other Mammals, *cf.* Corner, 9), which has resulted in the thickening and folding of the follicular wall, in the rupture of some of the thecal capillaries with consequent hæmorrhages into the theca externa and the follicular cavity, and in the rupture and disappearance of the membrana propria, that membrane becoming broken up partly by the formation of the ingrowths from the theca externa, partly by the localised invasions of theca-interna cells into the follicular epithelium. The breaking up of the membrana propria is no doubt accompanied by the rupture of some of the capillaries situated in it, and the resulting extravasations might well account for the blood that is found in the follicular cavity.

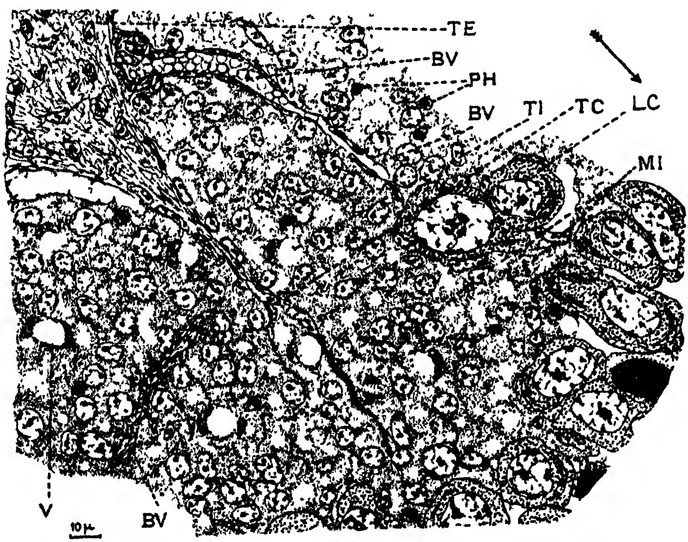
Corner (9) states that in the Pig, the theca interna is the layer most affected by the sudden collapse of the follicle after ovulation. In some of the folds resulting from the contraction, it is "violently torn apart" and its vessels "are not infrequently ruptured, with resultant hæmorrhage into the theca." When these hæmorrhages are large, they may burst through the granulosa into the follicular cavity. He discusses at some length the question of the constancy and importance of hæmorrhage into the corpus luteum in the Pig and other Mammals and comes to the conclusion that in the Pig, whilst not uncommon it "is the exception rather than the rule and is of no anatomical or physiological importance." With the latter part of this quotation we are in agreement, but so far as our limited material allows us to judge, the occurrence of such hæmorrhages into the follicular cavity would appear to be the rule in *Platypus*.

The presence in the follicular cavity of detached follicular (luteal) cells is also, we think, of no particular significance. Such cells have become separated, probably more or less accidentally, as the result of the folding of the epithelium and consequent dislocation of its cells, the enlargement of these latter and the passage between them of extravasated blood. Some of the detached cells already appear more or less degenerate, but the majority look normal and might well persist to form luteal cells.

The detailed structure of the follicular lining is illustrated in

Pl. IV. fig. 9 and text-fig. 6. The follicular epithelium (forming, as already noted, a quite irregular folded layer of very variable thickness and with a very uneven surface) consists of large deeply staining cells, of variable often compressed shape, polyhedral to cubical in the deeper parts, ovalish to pear-shaped more superficially, where they tend to be loosely arranged. They average in diameter ·026 × ·018 mm., and their nuclei, ·019 × ·012 mm., and are appreciably larger than the follicular cells of the ripe follicle, the corresponding measurements being 0·22 × ·015 mm., nuclei, ·0169 × ·0097 mm. Their cytoplasm is dense

Text-figure 6.




Portion of wall of corpus luteum. Stage I, A, showing the theca externa (*TE*) and its ingrowths (*TE* [1]), the theca interna elements (*TI.*) syncytial-like and vacuolated (*V*) and two cells in mitosis (*MI*), the luteal cells (*LC*) in process of differentiation and the ingrowing capillaries (*BV*). *PH.* Leucocytes. The arrow points towards the central cavity of the developing corpus luteum.

and finely granular, and there are indications of the presence of mitochondria such as occur in the cytoplasm of the definitive luteal cells. The nuclei, like the cytoplasm, stain deeply and exhibit precisely the same structure as those of the follicular epithelium (ante, p. 719), *i. e.* they possess an irregular karyosome, a well-marked reticulum, and numbers of minute ring-like nucleoli, whilst the large clear vesicular body or plasmosome recorded as occasionally present in the nuclei of the follicular cells is now of much more frequent occurrence.

An important advance on the intact follicular epithelium is now to be seen in the presence between the differentiating luteal cells of numbers of capillaries (fig. 9, *BV*), of relatively large size and situated not far below the irregular free surface, the epithelial cells lying in direct contact with their endothelial walls.

The theca-interna cells of the deep layer of the follicular lining (fig. 9, *TI*) are relatively small cells, the outlines of which in our preparations are only very occasionally visible. They vary somewhat in size but are much smaller than the luteal cells. Their nuclei average in diameter ·008 × ·006 mm.; they are ovoidal, stain rather deeply, and possess a central karyosome and a reticulum with peripheral chromatin-granules. The cytoplasm like that of the cells of the intact follicle is vacuolated, and not infrequently the cell-body is occupied by a single spherical vacuole, the fluid contents of which we are probably justified in regarding as of a secretory nature. This vacuolation of the theca-interna cells is much more evident in ovary I, C than in I, A, and as we shall see is also very marked in the theca cells of our Stage II. The theca-interna cells appear to be particularly active during the earlier stages in the formation of the corpus luteum, and in our view have a definite secretory function.

The question whether or not the follicular epithelial and theca-interna cells have actually increased in number by division subsequently to ovulation is one to which we are unable to provide a definite answer, at all events in the case of the first mentioned cells. It looks at first sight as if there had been a considerable increase in the number of cells in both layers and more particularly in the theca interna, but this apparent increase may simply be due to the fact that the cells, as the result of the marked contraction of the follicle, have become more heaped up over a much smaller surface area. We have not observed any definite evidence of mitotic division in the follicular epithelial (luteal) cells in this or any subsequent stage, and can only suggest that if such division occurs it must be limited to a quite short period just following ovulation when a sudden burst of division may accompany the release of the egg. Whilst we preserve an open mind in regard to the question of division of the follicular cells, in the case of the theca-interna cells we have definite evidence (text-fig. 6, *MI*) that mitotic division does take place, though it is not by any means abundant in our preparations. Without such mitotic division, it is difficult to account for the marked local thickenings which the layer exhibits.

The corpora lutea in the other ovaries of this stage call for no extended description since they are essentially similar to I, A.

In I, C, the theca-interna cells are, as already mentioned, more markedly vacuolated than in I, A, and they have invaded the deeper zone of the follicular epithelium to a somewhat greater extent. Detached cells are much less abundant in the follicular cavity than in I, A.

The corpus luteum of ovary I, D shows an advance on I, A in

the greater development of the ingrowths from the theca externa, some nine or ten being visible in a single section of the entire corpus luteum. They are not only more numerous than in I, A but extend farther inwards, with the result that the folding of the lining is markedly accentuated. The folds consist each of the central fibrous axis and along this are situated numerous theca-interna cells with small deeply stained nuclei, and forming the covering of the fold is an irregular layer of enlarged follicular epithelial (luteal) cells.

These fibrous ingrowths of the theca externa may be said to determine the general architecture of the corpus luteum. They are not mere passive folds, but active ingrowths of the theca externa and as they extend, the folding of the follicular lining becomes intensified and the follicular cavity becomes reduced to narrow clefts between the folds. The ingrowths at the same time serve as a framework along which the theca-interna cells spread and in which run many of the vessels supplying the luteal tissue. Finally, through the progressive enlargement of the luteal cells, the above-mentioned clefts between the folds become obliterated, and we have produced the solid corpus luteum as we find it in our next and succeeding stages. This mode of growth accounts for the indications of a rough pattern in the arrangement of the luteal cells which is sometimes recognizable in the fully-formed corpus luteum, the luteal cells showing a tendency to grouping in areas in relation to the fibrous ingrowths.

### Stage II.

Ovary of female No. 2, 9. ix. 05 (VIII), with two intra-uterine eggs, measuring 6·5 and 6·75 mm. in diameter, and after removal of shell, 4·5 mm. in diameter.

In the sections, the corpus luteum (including the theca externa) measures in diameter 4 × 3·12 mm., the luteal tissue alone measuring 3·9 × 2·75 mm. The ova are still solid and apparently in a late cleavage (blastodisc) stage.

Judging from the condition of the ova, this stage is separated from the preceding only by a relatively short interval, nevertheless the formation of the corpus luteum has, in that short time, made very marked progress. The whole structure has increased in size and it has become solid throughout, mainly as the result of the enlargement of the luteal cells, which have already attained at this relatively early period in the history of the corpus luteum, their maximum size.

In text-fig. 1, (*CL*) is shown a low-power view of a section of the entire corpus luteum. Comparison with Pl. IV. fig. 8, indicates at a glance the very striking advance which has been effected in the formation of the corpus luteum in this stage. Not only is the corpus luteum distinctly larger but the follicular cavity is now completely filled up by a solid mass of luteal tissue, whilst its opening is occupied by a projecting plug of the same tissue which is here freely exposed and devoid of any covering of

germinal epithelium. This protrusion of the luteal tissue has resulted from the rapid enlargement of the luteal cells inside the confined space of the collapsed follicle, no doubt facilitated by the large size of the opening through which the ovum escaped. In some cases, as in Pl. VII. fig. 13, the protrusion of luteal tissue is even more marked than in the present ovary, the plug having overflowed marginally to form a rim-like lip, overlapping the adjoining surface of the ovary.

A corresponding protrusion of the luteal tissue has been described by various authors for higher Mammals, by Sobotta (**39**) for the Rabbit, by O. van der Stricht (**44**) for *Vesperugo noctula* where he terms it "le bouchon épithélial obturator," and by Corner (**9**) who states that in many young corpora lutea in the Pig, the swelling of the granulosa cells causes a bulging of the corpus luteum tissue through the region of the follicular wall previously weakened by the rupture, the knob-like hernia so produced containing a tenth or more of the whole corpus luteum. In the Cow, he states, such a protrusion "seems to occur invariably and to persist throughout pregnancy, but in swine the hernia is not always produced, the whole wall of the corpus distending evenly instead."

In view of the relatively short developmental interval between this and the preceding stage, the advance in histological differentiation in the present stage is little short of remarkable. Indeed the corpus luteum may now be said to have attained the height of its histological development.

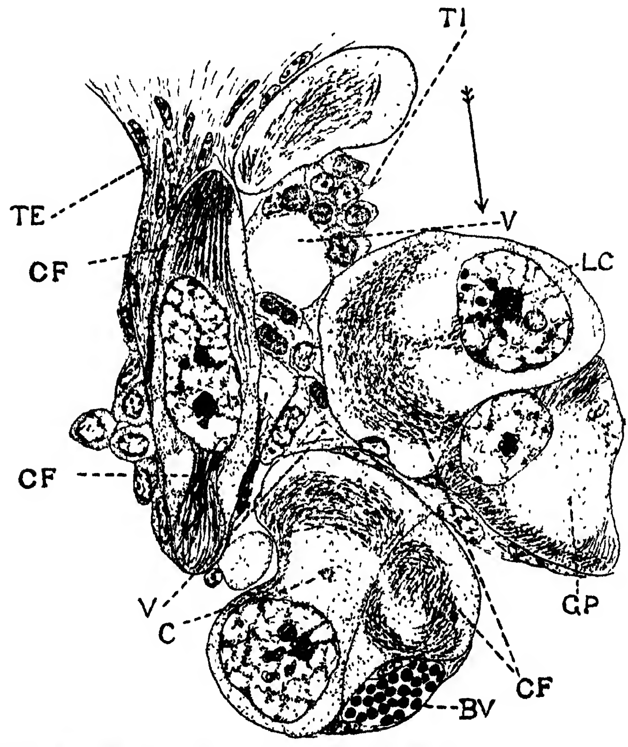
The luteal tissue (Pls. V. & VI. figs. 10 & 11, and text-fig. 7) consists of three cellular elements—(*a*) luteal cells which form by far the greater part of its bulk, (*b*) theca-interna cells, (*c*) fibroblasts which are derived, we believe, from those of the theca externa and which produce the fibrous network pervading the corpus luteum. In addition there is present a plexus of fine capillaries ramifying between the luteal cells.

The luteal cells, though varying considerably in size, show a distinct increase as compared with the follicular cells of the preceding stage, averaging ·024 × ·019 mm. in diameter as against ·019 × ·012 mm. in the latter. Here again we have seen no evidence of cell-division, and we conclude that the filling up of the follicular cavity as well as the increase in size of the corpus luteum as a whole are due in the main to the hypertrophy of the luteal cells.

As the measurements show, the luteal cells have now attained a relatively large size and are by far the largest elements in the corpus luteum. They vary in outline from spherical or polygonal to elongated elements, several times as long as broad. The cytoplasm is dense and very finely granular. In it are situated numerous elongated fibrillar mitochrondria (chondriocontes) specially abundant in the peripheral cytoplasm, though not confined thereto (fig. 11, and text-fig. 7, *CF*). In elongated cells they are specially obvious at the extremities, being disposed

parallel to their long axes. In cells more isodiametric, they tend to follow the contour of the periphery, sweeping round the nucleus. Usually an area free from mitochondria and composed of dense finely granular cytoplasm is left to one or other side of the nucleus. This area no doubt represents the position occupied

Text-figure 7.

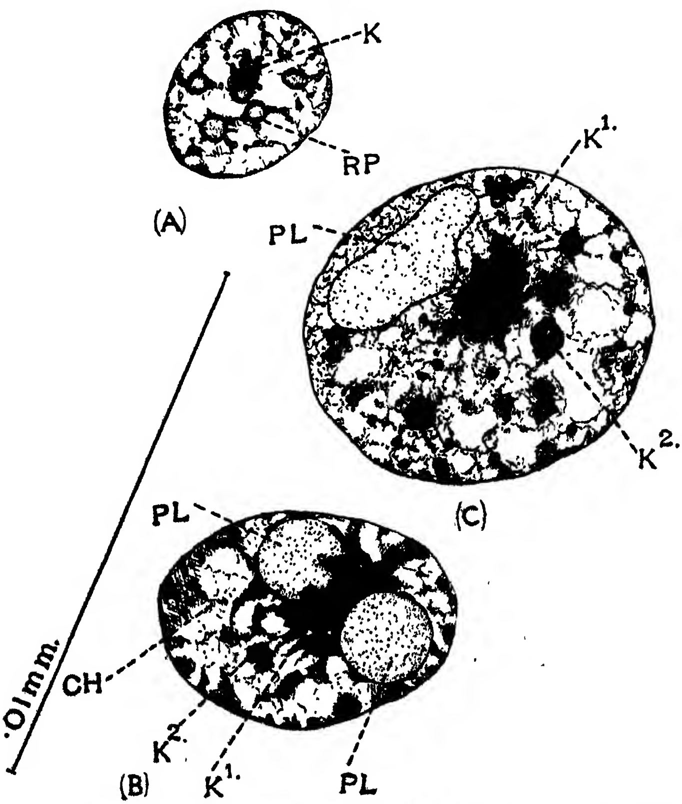



High-power view of small portion of corpus luteum, Stage II, to show the structure of the fully differentiated luteal cells (*LC*), *CF*. their fibrillar chondriocontes, *GP*. cytoplasmic area probably occupied by the Golgi apparatus now dissolved out. *C*. Centrosome granule. *TI*. Theca-interna elements, with vacuoles (*V*). *TE*. Theca-externa ingrowth. *BV*. Capillary.

by the dissolved out Golgi apparatus. A centrosome-like body may often be found in the middle of this area. The ground cytoplasm of the mitochondrial zone frequently appears of a clearer, much less dense character than the perinuclear cytoplasm. Exceptionally the cytoplasm of the luteal cell contains

a clear vacuolar space (rarely two), sometimes small, sometimes exceeding the nucleus in size and containing faint traces of a delicate reticulum. Such vacuoles become more abundant in later stages and are probably to be regarded as the expression of degenerative changes in the luteal cells. They are not to be

Text-figure 8.




High-power views to show the transformation of the nucleus of the follicular cell into that of the luteal cell. A. Follicular cell nucleus. B & C. Nuclei of luteal cells (Stage II). *K*. Karyosome. *RP*. Ring-nucleoli (plasmosomes). *CH*. Nuclear reticulum. $K^1$, $K^2$. Karyosomes. *PL*. Plasmosome.

compared with the fat-containing vacuoles in the luteal cells of the Eutherian Mammals. The nucleus (text-fig. 8, B and C) is large (·024 × ·019 mm. in average diameter), deeply staining, and in a highly active condition. It contains typically a large irregular mass of chromatin or karyosome and several smaller

masses ($K^1$, $K^2$), with all of which the well-marked and chromatin-rich reticulum (*CH*) is connected. In addition there are present one or two large clear vesicular bodies (plasmosomes) of spherical form and possessing a dark staining basophil membrane-like peripheral layer and a lighter staining centre (*PL*) as well as several smaller bodies identical with the "ring-shaped" nucleoli of the preceding stage. The spherical vesicular bodies above mentioned, the presence of which has already been noted in some few of the nuclei of the intact follicular epithelium as well as in those of the preceding stage, are now of pretty general occurrence, and are highly characteristic of the fully-developed luteal cells of this and succeeding stages. They are probably formed by the hypertrophy of the ring-like nucleoli.

Text-fig. 8 illustrates the changes during the metamorphosis of the nucleus of the follicular epithelial cell into that of the luteal cell. In A is seen the nucleus of a follicular cell. It is ovoid and contains two types of nucleoli: one is purely basophil and irregular in shape (*K*) and is always well-marked, the other (*RP*) is a curious ring-shaped, really a spherical plasmosome, with a basophil or amphophil cortex and an oxyphil or chromophobe medulla. There are usually several of these plasmosomes in each nucleus, and frequently one of them abuts against the karyosome. They are connected here and there by the chromatinic reticulum. Two stages in the transformation of these nuclei are shown in text-fig. 8, B & C. In B, there are two very large plasmosomes (*PL*), often showing a slight basophil edge and abutting against the hypertrophied karyosome ($K^1$). These plasmosomes, we believe, are derived from those (*RP*) of A. In C, a later stage is shown; the plasmosomes of B have run together to form one elongated body (*PL*), the hypertrophied karyosome ($K^1$) is present and also several smaller karyosomes ($K^2$). These latter may have arisen either from detached parts of the main karyosome or from ring-plasmosomes, in which case the medulla must have undergone absorption.

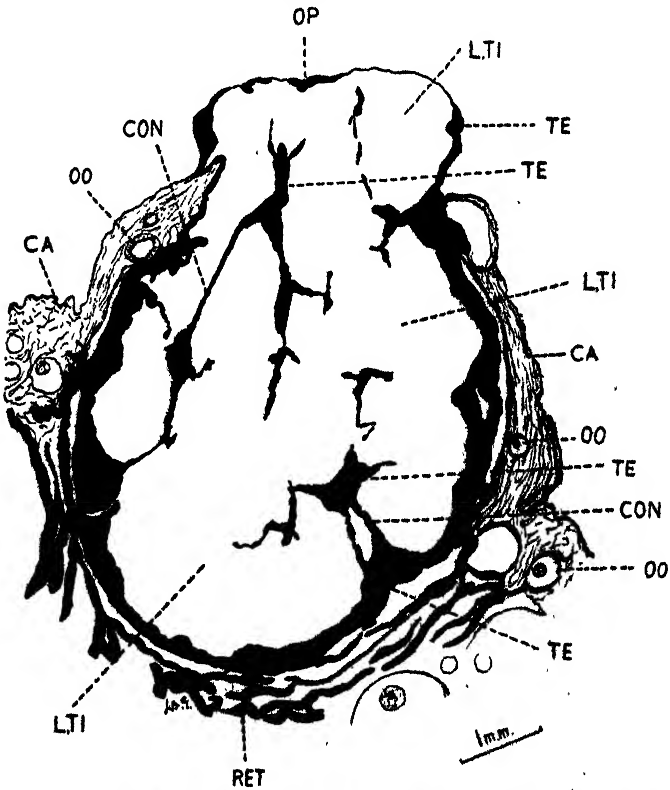
Whilst the hypertrophy of the luteal cells is, we think, the main factor in effecting the solidification of the corpus luteum, the ingrowths of the fibrous septa of the theca externa, accompanied as they are by the cells of the theca interna and by capillaries, are also contributory.

The theca externa in this stage has evidently undergone considerable stretching, consequent on the enlargement of the luteal cells, and the filling up of the follicular cavity. It is thinner than in the preceding stage and its inner surface presents a more even contour. From it arise the septal ingrowths, signalised as already present in the preceding stage, but now much more extensively developed.

They vary in thickness and in number (up to eight or nine may frequently be counted in one section), and extend for a longer or shorter distance into the luteal tissue as definite more or less radial septa before passing over into the delicate connective

tissue reticulum, presently to be mentioned, which pervades the entire corpus luteum and invests the individual luteal cells. Here and there in the luteal tissue there occur small irregular areas and strands composed of fibrous connective tissue only, evidently marking the sites of the clefts between the folds of the

Text-figure 9.




Low-power view of section of corpus luteum (Stage II), especially to show the theca externa and its trabecular ingrowths (drawn in black, *TE*), which support the luteal and theca-interna cells (*L*, *TI*, left white). *CA*. Cortical zone. *CON*. Connecting trabeculæ. *OO*. Oocytes. *OP*. "Plug" of corpus luteum. *RET*. Medullary zone of ovary.

lining of the preceding stage, whilst situated more or less centrally one such area takes the form of an elongated fibrous core of varying width (1·2 mm. in length by ·5 mm. in greatest thickness in one instance) which encloses the remains of the central blood-clot of the preceding stage. This core as well as

the other fibrous areas are in direct continuity with the connective-tissue reticulum of the corpus luteum. In our opinion, the septa, the just-mentioned fibrous areas, and the reticulum are all parts of one and the same connective-tissue system, and all owe their origin to the activity of fibroblasts derived from the theca externa.

The connective-tissue reticulum (clearly displayed in preparations of our next Stage III stained with Pasini's stain) takes the form of a fibrous network which, as already mentioned, extends throughout the corpus luteum and encloses the luteal cells in its meshes, the individual cells appearing to be completely surrounded and separated from their neighbours. Thin between the adjacent flat surfaces of the cells, the reticulum widens out in the angles between them and, indeed, wherever the cells are not in close contact; and in these places its reticular character as well as the nuclei of its fibroblasts are clearly displayed. What appear under the low power to be empty intercellular spaces between the luteal cells are seen under the oil immersion in suitably stained preparations to be occupied by the fine reticular network.

In the Pig, Corner (**9**, p. 175, fig. 25) has described the presence of "a reticulum of delicate connective-tissue fibrils" which form dense baskets round the granulosa and "theca lutein" cells. Inasmuch as the corpus luteum of the Pig consists exclusively, according to him, of these two types of lutein cell together with the endothelial cells of the capillaries, and as neither of the former exhibits any capacity to form fibrils and as no fibroblasts are present, Corner is led to suggest that the endothelial cells themselves lay down the reticular fibrils, a suggestion he upholds in a later publication (**11**). If Corner's conclusions for the Pig are correct, it follows that the interstitial connective tissue of the Monotreme is genetically different from the reticular tissue of the Pig, seeing that we have no reason to regard the fibroblasts, which are readily demonstrable between the luteal cells in *Platypus*, as other than the formative cells of the reticulum.

The theca-interna cells (Pls. V. & VI. figs. 10 & 11, *TI*) are highly characteristic elements histologically, and in this stage would appear to have attained their maximum functional activity. Though many of them have retained their original peripheral position between the theca externa and the luteal cells, where they form a discontinuous layer of very variable thickness, the majority of them lie along the septal ingrowths of the theca externa. Both peripherally and in relation to these ingrowths the cells occur massed together, the masses frequently presenting a sponge-like appearance owing to the presence of well marked intra-cellular vacuoles. We have already recorded the occurrence of vacuoles in these cells in the preceding stage as well as in the full-grown follicle, but in this stage they are not only larger but more numerous, and, indeed, here attain their maximum development.

The groups of theca-interna cells still present the same syncytial-like appearance noted in the preceding stage, cell-boundaries not being readily distinguishable. In many places, indeed, cell-outlines appear to be absent in our material, though here and there discrete cells may be observed on careful examination under high powers.

The nuclei of the theca-interna cells vary somewhat in size, averaging ·0078 × ·0059 mm., though a small proportion is distinctly larger. They differ in no essential respect from those of the preceding stage, and are still extremely granular and chromatic. In the cytoplasm of some of the cells a juxtanuclear chromatic cloud is visible. The origin of the vacuoles can be traced quite easily: in certain cells a clear space appears between the nucleus and the indefinite limiting cell-membrane, and this, growing larger, presses the nucleus into a crescentic shape until the whole cytoplasm and the nucleus form a cortex to the vacuole. In certain cases a fine coagulum can be noticed inside these vacuoles, but it is never so well marked as to fill the cavity.

## Stage III.

Ovary of female No. 3, 9. ix. 05 (X), with two intra-uterine eggs 6·75 and 7 mm. in diameter; after removal of shell and albumen, 5 × 4·5 mm. and 4·5 mm. in diameter respectively. The corpora lutea differ a little in size. The smaller one (including the theca externa) measures in the sections 3·38 × 2·34 mm. in diameter, the luteal tissue 3·2 × 2·18 mm. In the larger, the luteal tissue measures 3·7 × 2·18 mm. in diameter.

The ova, so far as can be determined, appear to be in much the same stage of cleavage (blastodisc stage) as those of Stage II.

We originally grouped this ovary with that of Stage II, but the corpus luteum proves to be in a slightly more advanced condition, and is of special interest since it exhibits the first onset of the regressive changes which becomes progressively more marked in later stages.

A low-power view of a section of the entire corpus luteum is seen in Pl. VI. fig. 12. A remnant of the central core of connective tissue still persists, whilst the free surface of the projecting plug or "propf." is now covered by a thin organised layer composed of clear parenchyma-like cells (two to four or more cells in thickness) which is in continuity with the septal prolongations of the theca externa. The plug region is fairly rich in capillaries, and in it, as in other parts of the corpus luteum, there occur occasional degenerate and collapsed luteal cells.

Cursorily examined, the luteal tissue does not appear to differ from that of Stage II. The luteal cells are of very much the same size as in the latter, perhaps a trifle larger (their average diameter being ·06 × ·037 mm.), whilst their nuclei (averaging ·027 × ·02 mm.) appear to be distinctly larger than in that stage. The cells are plump and active-looking, and their cytoplasm

and nuclei closely resemble in their characters those of the cells of the preceding stage. More careful study, however, reveals the presence of indications of commencing regression. In the connective tissue between the luteal cells, polymorpho-nuclear leucocytes are now present, though in no very great abundance. Here and there they have actually penetrated into the bodies of the luteal cells. This invasion is as yet quite sporadic, and only affects a very small proportion of the cells. Comparison with later stages indicates that this phagocytosis accompanies but does not directly bring about cell-regression. In the next two stages we shall find that whilst cell-degeneration is more advanced, leucocytic invasion is no more marked a phenomenon than in this stage.

Moreover, isolated shrunken and deeply-staining cells, obviously luteal cells in varying stages of degeneration, are now met with throughout the extent of the corpus luteum. Here and there we also encounter cells, the nuclei of which are undergoing vacuolization, and yet other cells in the cytoplasm of which are spherical spaces containing a deeply-staining homogeneous coagulum, but both of these phenomena are no more than indicated in this stage. The theca interna elements are disposed in syncytial-like groups internally to the theca externa and along the septal ingrowths of the latter as in the preceding stage, but their nuclei are here of slightly smaller average diameter, whilst vacuolization is much less marked than in that stage.

## Stage IV.

Ovary of female No. 1, 27. viii. 02, with a single blastocyst about 9 mm. in diameter in uterine portion of oviduct (Specimen Q of Wilson & Hill, **43**). Blastocyst with primitive streak (6 mm. in length) and very short head-process.

Diameter of corpus luteum (including theca) 3·8 × 2·75 mm. Diameter of luteal tissue 3·7 × 2·6 mm.

Although the developmental gap between this and the preceding stage is considerable, the general arrangement of the various elements of the corpus luteum does not differ in any marked way from that found in the earlier stages. There are now, however, evident signs of regression in the luteal cells.

The substance of the corpus luteum presents a more open appearance, more especially in the central region (Pl. VII. fig. 13). This is conditioned mainly by the larger size of the blood- and lymph-capillaries in this stage (Pl. VII. fig. 14, *BV*) as compared with those of the preceding stage. The luteal cells, moreover, have undergone shrinkage and are smaller than those of Stage III. Measurements show that there is an average shrinkage of ·013 × ·002 mm. in the diameter of the cells and of ·002 × ·001 mm. in the diameter of their nuclei as compared with those of the preceding stage.

Many of the luteal cells have assumed a more elongated,

spindle-shaped form, and their attenuated extremities and the enclosed mitochondria, which present a more broken-up, flocculent appearance, stain intensely with iron-hæmatoxylin, and appear under the low power as chromophile streaks distributed throughout the entire area of the corpus luteum (Pl. VII. fig. 14). This appearance is very characteristic of the present and the succeeding stage, in which latter, indeed, the degenerative process has gone so far that many of the luteal cells are represented simply by homogeneous masses stained of a jet-black colour (Pl. VIII. fig. 16).

Further evidence of regression is seen in the presence here and there of luteal cells, in the cytoplasm of which a clear spherical vacuolar space (rarely two) is present. Such spaces are devoid of formed contents and vary in size, the largest occupying half the cell-body. Of commoner occurrence than these cytoplasmic vacuoles are curious intra-nuclear vacuoles. Whilst the great majority of the nuclei of the luteal cells present a normal appearance, we meet not infrequently with others in which the nuclear contents seem to have disappeared, leaving a clear space bounded by the nuclear membrane. Careful examination shows that this condition in many cases at least, is brought about by a regressive change in the plasmosome. A small vacuolar space appears in the latter and increases in size, whilst the cortical membrane remains preserved. As the plasmosome grows, the nuclear contents are pushed to one side and ultimately are represented by remnants attached to the inside of the nuclear membrane. The original plasmosome continuing to grow, forms a large vacuolar structure which in the last stages occupies the whole space inside the nuclear membrane (*cf.* text-fig. 10, illustrative of the process in Stage V). Thus the degeneration of such nuclei is initiated by a change in the plasmosome. The process is not, strictly speaking, a chromatolytic one, since it is only in the later stages that the karyosomes and the chromatinic reticulum undergo dissolution.

The theca-interna elements do not appear to have altered in any definite manner, but their nuclei are slightly smaller as compared with those of the preceding stage, and whilst one can usually find a few vacuoles in the larger syncytial-like groups, it is certain that the number of these cavities has become much reduced.

Leucocytic invasion in this stage is extremely slight.

### Stage V.

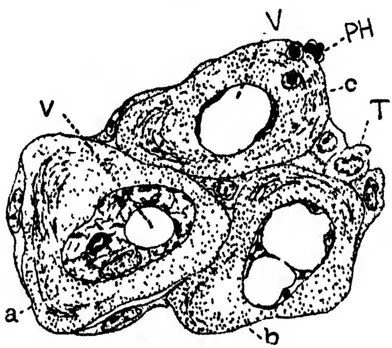
**Ovary (DQ.) 11·5 × 10 mm. in diameter, with two corpora lutea, each with a cicatricial dimple at apex, the one measuring 4·5 × 3·5 mm. in diameter, the other 5 × 3 mm. With two eggs in uterus, about 16·5 × 15 mm. in diameter. Embryo just a little older than Wilson & Hill's specimen H (43). Corpus luteum (including theca) in section 4 × 2·5 mm. in diameter; luteal tissue 3·8 × 2·34 mm.**

We are greatly indebted to Prof. R. A. Dart for the material of this stage.

The regressive changes described in the preceding stage have made further progress (Pl. VIII. figs. 15 & 16 and text-fig. 10). Though of much the same size as in the last stage the luteal cells present a more shrunken appearance, and the interstitial connective tissue around them has increased in amount.

In the luteal cells the degenerative changes are now very pronounced. The mitochondria, well preserved in the cytoplasm of the smaller oocytes in this ovary, have become profoundly altered in the luteal cells and have disappeared as precisely staining entities, all that remains of them being represented by darkly-staining streaks in the peripheral cytoplasm of some of the cells. Throughout the luteal tissue intensely-stained homogeneous masses are met with. These are completely degenerate

Text-figure 10.




High-power view of a group of three luteal cells (*a*, *b*, *c*) from Stage V, to illustrate the process of nuclear degeneration as the result of the appearance of intranuclear vacuoles (*V*). *PH.* Polymorpho-nuclear leucocytes. *TI.* Theca-interna cells.

luteal cells (Pl. VIII. fig. 15). Other cells destined to suffer the same fate, showing homogeneously-staining cell-bodies and darkly-staining pycnotic nuclei, are of common occurrence. Cells with nuclei showing various stages of nuclear vacuolization (text-fig. 10 and Pl. VIII. fig. 15) are also frequently seen. Indeed, the majority of the cells are now undergoing one or other form of regression, but, curiously enough, cytoplasmic vacuolization is less obvious than in the preceding stage.

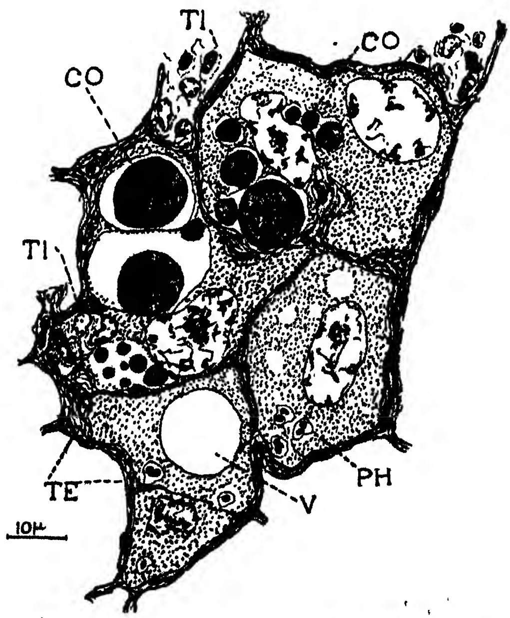
In correlation with the cellular degeneration which is in active progress, we now find that leucocytosis is extremely well marked. Numerous polymorpho-nuclear leucocytes are present in the interstitial connective tissue. They are of quite common occurrence in the cytoplasm, and are even found in the nuclei of the regressing luteal cells.

The theca-interna elements are still remarkably well preserved and show no signs of regression. Whilst bi- and multi-nucleate clumps of these elements are commonly met with (Pl. VIII. fig. 15), theca-interna cells with discrete outlines can now be seen without the least difficulty (Pl. VIII. fig. 16), and are here much more obvious than in any of the preceding stages.

## Stage VI.

Right ovary of *Echidna* (15. ix. 00) with recently laid egg. Ovary 17 × 7 × 6 mm., with single corpus luteum 4·5 × 3·5 mm. (Pl. I. fig. 2 and p. 729).

Text-figure 11.




High-power view of a group of luteal cells in process of regression, from Stage VI, to show especially the presence in their cytoplasm of colloid droplets (*CO*), vacuoles (*V*), and leucocytes (*PH*). *TI*. Groups of shrunken theca-interna cells. *TE*. Interstitial connective tissue of theca externa, now increased in amount.

A low-power view of an entire section of the corpus luteum is shown in Pl. IX. fig. 17, and highly-magnified views of the luteal tissue in figs. 18 & 19 and text-fig. 11.

The corpus luteum is in a fairly advanced stage of regression, the regressive changes being most marked in the central region.

Under low-power examination, the luteal cells present a much more diversified appearance than in any of the stages of *Platypus* previously described. This is due to the fact that the cells in many cases are shrunken and vacuolated and exhibit varying phases of degeneration. Moreover, the majority of them in the central region contain variable numbers of brightly-staining oxyphil spherules or droplets (Pls. IX. & X. figs. 18 & 19, *CO*). These vary not only in size but in their characters. The majority take the form of homogeneous spherules, colloidal-like in appearance, situated in vacuolar spaces in the cytoplasm; others, similarly situated and of similar appearance, instead of staining uniformly, possess a core which stains much more deeply than the periphery (fig. 18). The cell-body may contain one or two such spherules or a number (often considerable) of varying size. Where there are many, the cytoplasm is always greatly reduced and degenerate, and, indeed, all that may be left of the cell is the cell-membrane enclosing a space occupied by the spherules and remnants of the cytoplasm. When we first observed these spherules we were inclined to regard them as of the nature of secretory products of the luteal cells; but whatever relation, if any, they may have to the normal secretion of these cells, there can be no doubt they arise here as the result of a definite process of cell-regression. Miller (31) has observed colloidal droplets in the luteal cells of the human corpus luteum and has also regarded their occurrence as evidence of degeneration.

In addition to these colloidal spherules, there are numbers of much larger spheres, also occupying vacuolar spaces, which exhibit a finely granular structure (figs. 18 & 19, *GS*) and which look like areas of cytoplasm isolated by some peculiar process of cell-disintegration. Many of the cells also are vacuolated the vacuoles being devoid of formed elements or containing traces of granular contents.

The capillaries of the luteal tissue are still well marked (fig. 17, *BV*), and it should be mentioned that in some of them traces of a homogeneous oxyphil coagulum, which stains less intensely than the colloidal spherules, are present. A similar material also occurs in the lymph-sinuses of the medulla.

Round the periphery of the corpus luteum especially, we find many cells devoid both of spherules and vacuoles and with large nuclei of fairly normal constitution. Many of the nuclei contain one or two large plasmosomes, definitely limited and frequently staining homogeneously, almost like the colloid droplets in the cytoplasm (fig. 18, *PL*, and fig. 19). Vacuolated nuclei are not uncommon in the central region (fig. 19, *VN*); but, on the whole, nuclear vacuolization is in this *Echidna* stage a less-marked phenomenon than in the preceding.

The interstitial connective tissue of the theca externa is again extremely well developed (fig. 18 and text-fig. 11, *TE*), its strands enclosing and separating the individual luteal cells.

The theca-interna cells are, on the other hand, much less

conspicuous than in the preceding stage, but are still clearly distinguishable as small groups of cells situated here and there along the strands of the connective-tissue network (text-fig. 11, *TI*). Their nuclei now stain rather less intensely, and are less rich in chromatin granules than those of the preceding stage. Their cytoplasmic bodies are shrunken and ill-defined, and they are evidently now completely inactive. We have seen no evidence that the theca-interna cells ever take on fibroblastic activities.

A very striking feature in this corpus luteum, and one which affords clear testimony of its regressing character, is seen in the abundance throughout its substance of polymorpho-nuclear leucocytes. They are to be found in large numbers in the connective-tissue network, in the cytoplasm of the regressing luteal cells, in their nuclei, in the vacuoles, and in the colloidal and granular spherules (figs. 18 & 19, *PH*).

We possess another ovary of *Echidna* with a single corpus luteum, the structure of which is worthy of brief description.

The left ovary in this case was the functional one. It measured 15 mm. in length and 12·5 mm. in breadth, and the corpus luteum 5·5 mm. in height and 4·5 mm. in diameter.

We are indebted to Dr. Thos. L. Bancroft, of Eidsvold, Q., for the material. We are unable to give the size of the related uterine egg, but Miss C. J. Hill, who has examined sections of the uterus, informs us the uterine glands are very much in the condition of those of the uteri in our Stage I.

The interest of the corpus luteum of this ovary lies in the fact that it is of the vesicular type and contained a large central cavity, filled by a dense homogeneous coagulate recalling in its appearance and oxyphil-staining properties the colloid of the thyroid gland and the colloidal droplets of the regressing corpus luteum just described. The wall of the corpus luteum measures in maximum thickness ·64 mm. and in minimum ·22 mm., and its cavity approximately $3 \times 2{\cdot}4$ mm.

The luteal cells are large and well formed and not noticeably degenerate, though many of them, especially in the outer part of the wall, are vacuolated around their periphery. The nuclei contain karysomes and plasmosomes as in *Platypus*, and there is a juxta-nuclear cloud in the cytoplasm corresponding to a sphere, but mitochondria are not distinguishable. The interstitial connective tissue which is in direct continuity with the theca externa is strongly developed, and forms definite capsular investments round the individual luteal cells. Here and there along the strands of the theca externa, especially in the outer region of the wall, occur groups of small theca-interna cells, but vacuolization in these is not pronounced.

It is well known that in those Eutheria possessing a corpus luteum in which the antrum folliculi is rapidly occluded, a vesicular condition occurs in a percentage of cases. About 5 per cent. of the corpora lutea of the Cow are of this type (Gatenby).

In such examples the cavity is found to contain a thick coagulable fluid which is much denser than the liquor folliculi. The vesicular *Echidna* corpus luteum is an example of this exceptional type, and the thick coagulate in the cavity resembles in appearance that of the vesicular corpus luteum of the Cow. It has been assumed that this fluid represents or contains the secretion of the corpus luteum, but as to that we have no definite evidence of our own to offer.

## C.—Discussion.

We have made no serious attempt in this paper to deal with the vast literature relating to the formation and functions of the corpus luteum in the Mammalia. Adequate lists of the literature are provided in the papers of O. van der Stricht (**44**) and Long and Evans (**24**), and for an exposition of more recent views on the physiological aspects of the subject, the reader is referred to the reviews of Marshall (**28**), Corner (**10**), and Bouin (**6**), to the symposium on the œstrous cycle in the 'American Journal of Anatomy,' vol. xxxii., and to the papers of Robinson (**36**), Allen and his associates (**2**, **3**, **4**), Courrier (**12**), Gerlinger (**17**), Watrin (**45**), and others.

*Plan of Formation of the Monotreme Corpus luteum.*

| *Young Oocyte.* | *Full-grown Oocyte.* | *Functional Corpus luteum.* | *Regressing Corpus luteum.* |
|---|---|---|---|
| Follicular epithelium one-layered. | Follicular epithelium about two-layered, attains its maximum thickness. | Lutein cells without neutral fat granules. | Degenerate, with appearance of colloid droplets. |
| Primary theca. | Theca interna. | Vacuolated theca-interna elements, in syncytial-like masses and groups. | Still present, but in regression and no longer vacuolated. No evidence of transformation into fibroblasts. |
| | Theca externa. | Connective-tissue trabeculæ and pericellular connective tissue. | Increased in amount. |
| | Membrana propria. | Disrupted and no longer distinguishable. | |

### (1) *Formation of the Corpus luteum.*

The general plan of the formation of the corpus luteum in the Monotreme is shown in the above table.

In the Monotreme, the distinction between the three layers of the follicular wall of the full-grown follicle (viz. the theca

externa, the theca interna, and the follicular epithelium) is so definite and clear-cut that it is a relatively simple matter to follow their fate throughout the stages in the formation of the corpus luteum. We are consequently able to affirm that the lutein cells arise exclusively from the follicular epithelial cells as the result of hypertrophy accompanied by certain cytological changes, but no lipoid and no true fat are ever formed in them. We have never observed any evidence of mitosis in the follicular cells, and can only surmise that if they divide at all they must do so during a very brief period immediately succeeding the liberation of the ovum.

The fibrous theca externa early gives origin to actively ingrowing sprouts or trabeculæ which carry blood-, and no doubt also lymph-capillaries, though many of these enter the luteal tissue directly from the theca, and which not only furnish a connective-tissue framework for the support of the lutein and theca-interna cells, but provide a delicate pericellular investment around and between the individual lutein cells.

The theca interna of the mature follicle is a well-marked layer formed of polygonal cells with a characteristically alveolar cytoplasm, often definitely vacuolated. Immediately after ovulation the theca-interna cells multiply by mitosis and come to form syncytial-like masses and groups, situated partly in their original position between the lutein cells and the theca externa, partly along the ingrowths of the latter into the luteal tissue. They contain numerous vacuoles evidently filled during life by a clear fluid. The theca-interna elements are already prominent in our Stage I, and they reach their maximum development in Stage II. In the succeeding stages, vacuolization becomes less marked; in Stage V the cells are still well preserved and many of them have acquired discrete outlines. In Stage VI they are still recognizable, but are evidently inactive and in process of regression.

It seems difficult to avoid the conclusion that these theca-interna elements subserve in the early corpus luteum a definite secretory function which may, of course, simply be an intensification of that carried out by the theca-interna cells of the intact follicle. We have no evidence that they ever take on a fibroblastic activity, even in the regressing corpus luteum.

## (2) *Cytology of the Luteal Cell.*

One of the most characteristic features of the Eutherian luteal cell is the presence of globules formed of an osmiophil fat. Thus treatment of the luteal cells with osmium tetroxide will reveal a fine fatty granulation in the cytoplasm even in cells in the early invasion stages. In the human corpus luteum of menstruation, Gatenby (15) has shown that these granules are disposed after the manner of the mitochondria of many gland-cells, and at one period stain equally readily by osmium reduction and by iron-hæmatoxylin. He suggests the granules may be of mitochondrial

origin, but our knowledge of the cytology of the luteal cells is still scanty, and further work is necessary before precise statements as to the origin of these osmiophil globules can be made.

In view of the invariable occurrence of such globules in the Eutherian luteal cell, it is a fact of interest that they are entirely absent in the luteal cells of *Platypus*. Some of our material had been fixed in Flemming's fluid, and we can confidently state that osmiophil lipoid is not present nor do vacuoles appear in the cytoplasm in the best fixed luteal cells in our collection. In the marsupial, *Didelphys aurita*, we have been able to examine sections of quite young corpora lutea after Flemming fixation. In the luteal cells there are present in no great abundance droplets of varying size which have stained of a brownish grey tint with the osmic acid of the fixative, and which would seem to represent the lipoid of the luteal cells in *Eutheria*. In favourable sections the appearances suggest that these droplets originate from small ring-like granules which may possibly be mitochrondrial in nature.

Certain observers have regarded the degree of development of these osmiophil globules in the luteal cells as an index of functional activity. Our observations, however, indicate that the secretory activity of these cells can be carried on in the entire absence of such globules.

Our observations on the cytology of the luteal cells of *Platypus* have necessarily been limited by the material available, but we have been able to show that there is present a large juxta-nuclear area, in the centre of which a centrosome-like granule can sometimes be made out. We believe that this area marks the site of the dissolved-out Golgi apparatus, and that consequently a Golgi apparatus similar to that in human, rat, mouse, and guinea-pig luteal cells, is present in *Platypus*.

Another remarkable feature in the fully-differentiated luteal cell of *Platypus* is the presence of numerous large mitochondria in the form of long filamentous elements or chondriocontes which sweep round the cell, lying between the juxta-nuclear cytoplasmic area and the periphery. Regaud and Policard (**35**) were, we believe, the first observers to record, in the case of the Hedgehog, the existence of filamentous mitochondria in luteal cells. There can be no doubt that one of the most important events in the transformation of the follicular epithelial cell into the luteal cell is the hypertrophy of the mitochondria, for in the sections in which the filamentous mitochondria in the luteal cells are clearly visible, we have failed to observe them in the follicular epithelial cells. This, we believe, is not because the latter do not contain them, but because they are so delicate that they have not been preserved by the fixative employed.

Robinson (**36**) states that in the flattened epithelium of the early follicles in the Ferret, granular mitochondria are present, but as the follicles increase in size, the mitochondria "assume the form of granular rods or filaments."

The nucleolar complex of the luteal cells, like that of all glandular cells, is also of interest. The nucleus of the fully-formed follicular epithelial cell possesses a number of peculiar ring-like nucleoli and generally one irregular karyosome. In the fully-formed luteal cell, besides the main karyosome, there is present another type of karyosome, in the form of smaller elements, sometimes solid, sometimes with a lighter centre which may have arisen from the ring-nucleoli by a process of thickening of the peripheral ring at the expense of the medulla. In addition the nucleus contains one or more clear vesicular bodies or plasmosomes which would also appear to be derived from the ring-nucleoli. A common origin of both plasmosomes and karyosomes from a primitive nucleolus has been described by Jorgensen (**23**) and by Ludford (**26**) in Molluscs.

(3) *The Corpus Luteum in relation to the Monotreme Life-cycle.*

In view of the position of the Monotremes at the base of the Mammalian series, it may not be devoid of interest to correlate the phases in the formation and functional activity of the corpus luteum with the periods of embryonic development, and to see in how far the results correspond with those similarly obtainable for the higher Mammals.

First of all, a brief outline of the embryonic history of the Monotremes. The yolk-laden telolecithal ovum, when shed from the ovary, has a diameter of about 4–4·5 mm. It possesses at the animal pole a small germinal disc and is invested by a thin zona. It is received into the Fallopian tube and there fertilized, and as it passes down the tube it becomes enclosed, outside the zona, first of all by a coat of albumen and then by a shell-membrane, at first quite thin but becoming thicker later on. The intact egg in its envelopes appears to vary in diameter from about 5 to over 6 mm. It passes into the enlarged uterine segment of the oviduct, which is richly provided with highly active glands, and therein it undergoes meroblastic cleavage and the succeeding phases of development up to the time of laying. As soon as the ectoderm has grown round and enclosed the yolk, it commences to enlarge, and eventually forms a large blastocyst, filled with the nutritive fluid absorbed from the uterine lumen and the more or less disseminated yolk-spheres of the original yolk-mass of the ovum. The egg enclosed in its shell reached a diameter of round about 16·5 × 15 mm. in *Platypus*, and is eventually laid when the embryo in *Echidna* (and the same probably holds true for *Platypus*) has attained a stage of development roughly comparable with that of a chick of 38–40 hours' incubation and possesses some nineteen pairs of somites. After an unknown period of incubation, in the nest (*Platypus*) or in the pouch or incubatorium (*Echidna*), the young Monotreme, about 16·5 mm. in length in *Platypus* and about 12·5 mm. in *Echidna*, emerges from its enclosing shell and egg-membranes with the aid of its

caruncle and egg-tooth, and proceeds to subsist on the milk which exudes from the mammary glands of the mother, the tubules of which have already attained a length of about 5 cm. some time before the egg is laid (Hill & Martin, 21).

We can thus distinguish in the development of the Monotreme three periods, viz. (1) a period of intra-uterine development, (2) a period of incubation, and (3) a period of lactation.

If, now, we proceed to correlate the phases in the history of the corpus luteum with these developmental periods, we see from the data recorded in the preceding pages that this is a very simple task, for the corpus luteum in the Monotreme not only attains its full growth and activity during the uterine period, but exhibits evident signs of regression by the time that period is completed, so that whatever the functions of the corpus luteum, they must become effective remarkably early, certainly by the time the blastocyst is formed.

The history of the Monotreme corpus luteum itself may be resolved into three main periods. There is first of all the early period characterized by the remarkable multiplication and the glandular activity of the theca-interna cells, which is at its height when the lutein cells are already well differentiated. This period comprises our Stages I and II and covers the time from just before ovulation and just after ovulation until cleavage is completed.

This early period is followed by a second which overlaps the first, in which the intra-cellular vacuoles of the theca-interna elements are much less conspicuous, whilst the lutein cells reach the height of their cytological development. This period is represented by our Stages II, III, and IV, and extends from the completion of cleavage up to the formation of the blastocyst and the first appearance of the primitive streak.

The second period is succeeded by a final period of regression in which the luteal cells exhibit obvious signs of degenerative change both in their nuclei and cytoplasm, the most prominent features of which are colloidal and granular degeneration of the cytoplasm of the lutein cells, vacuolization of their nuclei, marked leucocytic infiltration and increase of the connective tissue. In the Monotreme regression appears to set in remarkably early. Degenerative changes are already evident in our Stage IV, and they are well advanced by the time the egg, containing the early embryo, is laid.

From the literature of the subject we have compiled the following data as to the history of the corpus luteum in other Mammals. In the Marsupial, *Dasyurus*, Sandes (37) states that the corpus luteum attains its full development at the time when blastocysts 6·5–7 mm. in diameter (primitive streak and head-process stage) are present in the uteri. It remains in the same state for 7–8 weeks after the birth of the young, then it begins to regress. According to Sandes, the chief factors in regression are fatty degeneration of the luteal cells and their removal by

leucocytes, atrophy of the blood-vessels, and increase of the connective tissue to form a corpus fibrosum. By the time the young one is about 10 cm. long, some four months after birth, "there remains no trace of the corpus luteum in the ovary, which is found to be full of young ova beginning to grow in preparation for the next œstral period." The records of Hill (**19**) show that the lips of the pouch-young become free at 7–8 weeks after birth, *i.e.* about the time regression of the corpus luteum sets in, according to Sandes, and that the entire lactation period extends over about four months. In his paper on the œstrous cycle in the Opossum, Hartman (**18**) calls particular attention to the statement of Sandes as to the long persistence of the corpus luteum in *Dasyurus*, since he finds that in *Didelphys* the corpus luteum "declines much more rapidly than that of *Dasyurus*. . . . . . At parturition, or about twelve days after ovulation, the corpus is already infiltrated with swarms of leucocytes and numerous connective-tissue cells." Later on in his paper, Hartman states that "the corpora lutea degenerate soon after parturition; in four or five weeks they have all but disappeared." Whether this remarkable difference in the time of regression of the corpus luteum in these two Polyprotodonts is related to a possible difference in their sexual cycles is a question which must remain in abeyance until we know whether *Dasyurus* is really monœstrous, as Hill and O'Donoghue (**20**) originally thought, or polyœstrous like *Didelphys*, and also until we possess precise information as to the histological condition of the corpus luteum of *Dasyurus* at the time of parturition.

The important monograph of Long and Evans (**24**) on the œstrous cycle in the White Rat provides valuable details as to the history of the corpus luteum in this rodent. Their observations show that at their Stage V (some 4 days after the start of the cycle and 2–3 days after ovulation) the corpora lutea are normally fully formed and in vigorous function. At about the same time—according to Huber (**22**) towards the end of the fourth day after insemination—the morulæ pass from the tubes into the uteri and enter on the stage of early blastocysts. The corpora lutea remain fairly constant up to almost the middle of pregnancy, but after the tenth day they increase in size (reaching up to just under 2 mm. in diameter towards the end of gestation). This increase results chiefly, if not entirely, from the growth of the lutein cells. Towards the end of pregnancy and immediately after parturition, marked changes are observable in the lipoid contents of the lutein cells. The lipoid granules at this time increase greatly in number and some of them markedly enlarge, so that they exhibit a distinct inequality in size. The authors regard these alterations in the lipoid contents as indicative of the cessation or the diminution in functional activity of the lutein cells. After parturition the corpora lutea undergo diminution in size, though they persist throughout the period of lactation, which lasts from twenty-one days to double that time

if the young are left with the mother. Twenty days after parturition, they still measure somewhat over a millimetre in diameter, though the number of lutein cells is considerably diminished. At about one hundred and twenty-five days after parturition, the authors state that, with the aid of their vital dye technique, they were able to distinguish the last quite degenerate vestiges of these corpora lutea graviditatis.

In the case of the Mouse, Sobotta (**38**) states that the corpus luteum attains its definitive structure 60–72 hours after ovulation. At that time, eggs in the 8–16-celled cleavage stages are present in the Fallopian tubes. In later stages the only alterations that take place are an increase in size of the luteal cells, and the appearance in them of fine fat granules in varying numbers. According to Sobotta, a regression of the corpus luteum does not occur in the Mouse, but it is difficult to believe that the Mouse should in this respect differ so fundamentally from the Rat. In the Rabbit, Niskoubina Nadiejda (**32**), quoted by O. van der Stricht, distinguishes (1) a period of development of the corpus luteum extending over 4–5 days after coition (5 days according to Sobotta (**39**)), and this is followed by (2) a period of full functional activity of 9–10 days duration and finally (3) a regressive period which supervenes towards the middle of pregnancy. From the 14th–15th day on, the corpus luteum is said to be a "vestigial organ." Regression is characterized by a reduction in size of the lutein cells and their eventual disintegration following on fatty degeneration, by the increase of the connective tissue and atrophy of the vessels, and by leucocytic invasion of the luteal tissue. Cohn (**8**) states that the lutein cells attain their maximum size at 8 days, whilst Marshall (**30**) says that at that time the corpus luteum is "very nearly fully formed." At 8 days there are blastocysts in the uteri varying somewhat in their degree of development from primitive streak to flat embryo stages. They have a temporary attachment over the antembryonal pole, and in those more advanced the definitive ecto-placental attachment is being effected.

In the Bat, *V. noctula*, O. van der Stricht (**44**) also distinguishes three phases in the history of the corpus luteum:—1. A phase of genesis, extending from ovulation up to the fixation of the blastocyst, during which the lutein cells are formed mainly from the follicular epithelium, but partly also from interstitial elements of the theca interna. 2. A phase of full establishment, characterized by the very rich fat-content of the lutein cells, which the author regards as an index of functional activity. At the beginning of this phase the lutein cells gradually increase in size, reaching their maximum at the mid-period of gestation, when they remain constant almost up to the close of the latter. 3. A phase of regression and atrophy which begins some time before the birth of the fœtus, and is characterized by the diminution in size and number of the lutein cells and the hypertrophy of the connective tissue.

Corner (9), in the case of the corpus luteum of the Pig, states that it reaches its full development on the 8th–10th day, when unattached blastocysts are present in the uterine horns. The blastocysts become attached between the 10th and 15th days, and in those cases where the ova have not been fertilized the corpus luteum begins to regress after the 15th day. Otherwise, in normal pregnant females it persists, and only commences to undergo regression about the time of parturition.

It is clear, then, that we can distinguish in the history of the corpus luteum a period of functional activity which culminates in the attainment by the organ of its maximum histological development. This is usually attained relatively early, by the time the blastocyst stage is reached and the attachment of the same (if any) is being accomplished. Then follows a period of regression which begins in the latter part of the gestation period, usually some time before parturition, and therefore prior to the functioning of the mammary apparatus, and which results in the atrophy of the glandular cells and the more or less complete disappearance of the organ.

Our investigations show that the corpus luteum of the Monotreme does not differ in any fundamental respect, so far as its general history is concerned, from that of other Mammals. We have described a corresponding period of functional activity, and have attempted to differentiate between an earlier phase of theca-interna cell-activity and an overlapping but somewhat later phase of lutein cell-activity. We have also described a corresponding period of regression, the regressive changes being well marked by the time the egg is ready for laying.

But there is one point of difference in detail which is perhaps worthy of notice, and that is that regression sets in at a much earlier stage of embryonic development in the Monotremes than in other Mammals and a considerable time before the mammary apparatus comes into use. Indeed, judged by the stage of development of the embryo in the newly-laid egg, it would seem as if the period of functional activity of the Monotreme corpus luteum was extremely short, but we have, unfortunately, no knowledge of the rate of development in Monotremes. It may be comparatively slow like that of Reptiles, and is almost certainly slower than that of other Mammals.

Various authorities—Sobotta (40), Marshall (37), and others—have called attention to the remarkable rapidity with which the corpus luteum attains its completed form in the Mammals generally. The Monotremes appear to conform to this general rule, though here again we can only judge of time in terms of developmental progress.

### (4) *The Follicular Epithelium and Theca interna, their functional significance before and after ovulation.*

In the earlier part of this paper we have shown that it is only when the oocyte is completing its growth that the follicular

epithelium enlarges and becomes a conspicuous layer. At this time also, the theca-interna cells form an important constituent of the follicular wall. These facts are, we think, deserving of special emphasis.

The oocyte of the Monotreme undergoes in the ovary a very noteworthy growth from a cell of microscopic dimensions to a relatively huge cell 4–4·5 mm. in diameter; and it is a remarkable fact that the follicular epithelium and the theca interna, instead of becoming flattened out and attenuated during this enormous growth, actually increase and attain their maximum development around the oocyte shortly before ovulation takes place. The facts that this increase has no obvious direct relation to the growth of the oocyte, and that both layers, whilst glandular in character, are very distinct histologically, suggest the question whether each of these layers may not have, in addition to its prospective significance in corpus-luteum formation, some definite functional rôle to play prior to ovulation. That these two layers have a nutritive function in relation to the growing oocyte is admitted. The question is whether in the full-grown follicle one or other or both may not have acquired some other function. That, of course, is a question impossible to settle on histological grounds alone, but certain considerations in regard to it appear to be worth setting down.

In the first place, we have the fact that the follicular epithelium attains its maximum development as such around the full-grown oocyte, and the further fact that after ovulation the follicular cells undergo marked hypertrophy to form the luteal cells. In view of the cytological differences between the two, we may well suppose that they have quite different functions. As concerns the theca-interna cells, there are no such marked differences in *Platypus* between these elements in the intact and ruptured follicle as are seen in the case of the follicular and luteal cells, and, moreover, they would seem to attain their maximum glandular activity shortly after ovulation and whilst the corpus luteum is in process of formation. That being so, we conclude that the theca-interna cells function as well before as after ovulation, but are most active after the latter event.

It has been maintained by various observers—Robinson (36), Marshall & Wood (29), Allen (2), Allen and his co-workers (3), Hartman (18), and Courrier (12)—that the ovarian follicle, and in particular the follicular epithelium, is responsible for the production of a hormone ("folliculine," Courrier) which is present in the liquor folliculi and which induces the condition of œstrus. A discussion of this problem is outside the scope of this paper. All we need say is that our observations on the Monotreme follicular epithelium are not in disaccord with this view, and that, in the absence of a fluid-filled Graafian follicle, the secretion, if it is produced by the follicular epithelium, must be passed directly into the capillaries of the theca interna. Allen and his co-workers (4) have stated that "the ovarian follicular hormone

can be extracted from ovaries of laying hens," where also the follicles are solid, but they say definitely they were unable to obtain it from full-sized follicles.

On the other hand, Zondek and Aschheim in a recent paper (**46**) have come to the conclusion that the seat of origin of the œstrous hormone is in the theca-interna cells. They point out that, in the human ovary, these cells are very active from an early stage of the follicle, and they produce experimental results which, in their view, demonstrate that the granulosa cells of the follicle give a negative reaction so far as inducing œstrus is concerned, whilst the theca-interna cells yield a positive one. If the results of these observers are substantiated, we should still have to account for the remarkable development of the theca-interna elements in the Monotreme which succeeds ovulation, and we should be forced to the conclusion that in the corpus luteum they must have quite another function. On the other hand, the histological evidence in the Monotreme leads us to conclude that they continue to produce in the early corpus luteum the same secretion as in the full-grown follicle, but what the precise function of that secretion is we can only speculate. If we assume that one of the functions of "folliculine" is to produce a condition of general hyperæmia in the genital tract, we might suppose that the secretion of the theca-interna cells served to activate the glands of the Fallopian tube and uterus. This would explain the continued activity of these cells after ovulation, since it is, of course, only after that event that the albumen and shell are secreted around the ovum, whilst it is some little time after the formation of these secondary egg-membranes that the uterine glands reach their maximal secretory activity (C. J. Hill).

But the time is not yet ripe for a precise evaluation of the hormonal functions of the glandular constituents of the ripe follicle and the corpus luteum in the Mammals generally, and renewed investigations, with the appropriate technique, on the history of the theca-interna cells in higher Mammals are very desirable, in view of the conflicting statements on this subject which abound in the literature.

Certain observers—O. van der Stricht (**44**), Corner (**9**), Gatenby (**15**), Solomons & Gatenby (**41**)—have shown that in the Mammals studied by them the theca-interna cells take a no inconsiderable part in the constitution of the fully-formed corpus luteum. According to the two observers first mentioned, they give origin, in the Bat and in the Pig respectively, to glandular cells closely resembling the luteal cells of follicular epithelial origin (so-called theca-lutein cells), whilst, according to the last-named observers, they give rise to the characteristic "stellate cells" of the human corpus luteum.

On the other hand, Sobotta (**38**), who is a strenuous supporter of the exclusive derivation of the lutein cells from the follicular epithelium, maintains that the theca-interna cells become transformed into connective-tissue fibroblasts, a view held by quite a

number of other investigators. Togari (**42**), however, who has more recently re-investigated the formation of the corpus luteum of the Mouse, fails to support Sobotta's statement. He finds that the theca interna of the mature follicle is formed of a layer of polygonal cells, one to two cells thick, the cytoplasm of which "resembles a honeycomb with fat-like substance." After ovulation, the layer becomes of irregular thickness. Its cells remain in their original position at the periphery of the developing corpus luteum, and several hours after ovulation, some of them show signs of degeneration. This degeneration becomes more and more evident, until eventually they disappear completely about sixty hours after parturition, so that no trace of them is to be found in the full-grown corpus luteum. Togari affirms that the polygonal cells of the theca interna reach their maximal differentiation before the rupture of the follicle. He supports the view that they are nutritive in function, though he thinks "their increase contrary to the decrease of the granulosa cells in the atretic follicle suggests their secretory function," a conclusion we do not pretend to be able to follow.

O'Donoghue (**33**) has called attention to the variation in the degree of development of the theca interna in Marsupials. He finds it best marked in *Phascolomys wombat*, where it is composed of rather elongated polygonal cells arranged three or four deep, and in this respect it approaches the condition in many Eutheria. At the other extreme is *Dasyurus*, in which he states that, although it is easily recognizable in the young follicle, it is almost indistinguishable from the theca externa in the ripe follicle. We have examined preparations of both *Dasyurus* and *Didelphys*, and find, like O'Donoghue, that in the full-grown and nearly full-grown follicles, the theca interna is remarkably thin and scanty as compared with that of *Platypus*, while in younger follicles it appears as a quite well-marked layer, in places approximating in thickness to the follicular epithelium. It would seem, however, from the information available, that the thecal activity in the Marsupials is on somewhat different lines from that of the Monotremes, since Sandes (**37**) states that the theca interna forms only the vascular connective tissue of the corpus luteum, whilst O'Donoghue (**33**) likewise thinks that it is largely used up along with the theca externa in forming the connective-tissue ingrowths, even if some of its cells are still existent in the completed structure.

In any case, we have shown that in the corpus luteum of the Monotreme there are two sets of apparent glandular elements, perfectly distinct developmentally and cytologically, viz. the theca-interna cells which attain their maximum activity quite early in the history of the corpus luteum, and the lutein cells which reach their maximum differentiation later than the theca-interna cells and which function throughout the greater part of gestation.

Now, whilst the ovarian follicle and in particular the follicular

epithelium is held to be responsible for the production of the œstrous hormone, the corpus luteum is by many authorities believed to have two main functions: (*a*) to produce a secretion which inhibits the formation of full-grown follicles, and therefore the onset of œstrous during pregnancy; (*b*) to produce a growth-stimulating hormone which induces growth of the uterus and of the mammary apparatus. We have no intention here of entering into any further discussion of this much-debated problem, but would merely emphasize the fact that in this paper we have provided from the histological aspect strong evidence in favour of the conception of a double secretory function of the corpus luteum at slightly different periods in its life-history. Such a conception, we may add, provides an explanation of some of the confusing and apparently contradictory results obtained by the use of corpus-luteum extracts, not only by physiologists but by gynæcologists.

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## EXPLANATION OF THE PLATES.

*List of common Reference-letters.*

*BV.* Blood-vessel or capillary.
*CC.* Connective tissue core of corpus luteum.
*CF.* Chondriocontes.
*EB.* Extravasated blood.
*FC.* Follicular epithelium.
*LC.* Luteal cell.
*LS.* Lymph-sinus.
*OO.* Oocyte.
*OP.* Opening or "plug" of corpus luteum.
*PH.* Leucocyte.
*PL.* Plasmosome.
*RET.* Trabeculæ of medullary region of ovary.
*TE.* Theca externa.
*TE*[1]. Ingrowths of theca externa.
*TI.* Theca interna.
*V.* Vacuoles.
*YE.* Yolk-spheres.
*Z.* Zona pellucida.

Figures 1 and 19 are the same size as the original photographs; the remaining figures have been very slightly reduced.

### Plate I.

Fig. 1. Left ovary of *Platypus*, Stage I, C, with two corpora lutea. For explanation see text, p. 728. × about 8.

Fig. 2. Right ovary of *Echidna*, Stage VI, with a single corpus luteum. For explanation see text, p. 729. × about 8.

### Plate II.

Fig. 3. Follicular wall of oocyte about full-grown, measuring 4·3×4·1 mm. in diameter. The yolk-spheres (*YE*) of the oocyte are seen in the upper part of the figure. *BV.* Capillaries in theca interna and membrana propria. *FC.* Follicular epithelium. *MP.* Membrana propria. *TI.* Theca interna. *TE.* Theca externa. *Z.* Zona. × 350.

Fig. 4. Portion of medullary region of ovary of *Platypus* (III, *a*, 19.viii.01), showing the trabeculæ (*RET*) carrying blood-vessels (*BV*), the lymph-sinuses (*LS*), many of them containing a coagulum, and on the left side of the figure, a small portion of a follicle.

## Plate III.

Fig. 5. Portion of medullary region of ovary of *Platypus* (H) to show the presence of disintegrating yolk-spheres (*YE*) in the lymph-sinuses (*LS*). *RET.* Trabeculæ. *BV.* Blood-vessels. × 150.

Fig. 6. Portion of ovary of *Platypus*, Stage V, showing an atretic follicle in process of discharging the disintegrated remains of the oocyte (*DO*) into an underlying lymph-sinus (*LS*) through a break in its wall. *FC.* Follicular epithelium. *IZ.* Inner zone of theca. *OO.* Oocyte. *TE.* Theca externa. × 50.

## Plate IV.

Fig. 7. Portion of ovary of *Platypus*, Stage II, showing a more advanced stage in follicular atresia. *FC.* Follicular epithelium. *LS.* Lymph-sinus. *OO.* Oocyte. *PO.* Opening in follicular wall, through which contents are discharged. *TE.* Theca externa. *YE.* Yolk-spheres. *Z.* Zona. × 50.

Fig. 8. Low-power view of section through the corpus luteum of Stage I, A. *EBH.* Extravasated blood in cavity of corpus luteum and in theca externa. *BV.* Blood-vessel. *LC.* Luteal (follicular epithelial) cells. *LS.* Lymph-sinus. *OP.* Opening of cavity of corpus luteum, through which oocyte escaped. *OO.* Oocyte. *TI.* Theca interna. *TE.* Theca externa. The arrow indicates the part of the wall which is seen under higher magnification in fig. 9. × 34.

## Plate V.

Fig. 9. Portion of the wall of the corpus luteum, Stage I, the position of which is indicated by the arrow in fig. 8. *BV.* Capillaries. *LC.* Luteal cells. On the left of figure are detached luteal cells in the follicular cavity. *TI.* Theca-interna cells. *TE.* Theca externa. *TE*[1]. Ingrowth of theca externa. × 230.

Fig. 10. Peripheral portion of the corpus luteum, Stage II, showing the theca externa (*TE*) containing a blood-vessel (*BV*) and giving off an ingrowth (*TE*[1]), the theca-interna cells (*TI*), vacuolated, and the luteal cells (*LC*) containing chondriocontes (*CF*) and separated by interstitial connective tissue, in which run capillaries (*BV*). × 230.

## Plate VI.

Fig. 11. Another portion of the periphery of the corpus luteum, Stage II, showing the theca externa (*TE*), the theca interna (*TI*) forming a layer of irregular thickness, syncytial-like in character and containing large vacuoles (*V*) and the luteal cells (*LC*) with chrondriocontes (*CF*). × 350.

Fig. 12. Low-power view of section through the corpus luteum, Stage III. *CC.* Remains of blood-clot and connective-tissue core. *LC.* Luteal cells. *LS.* Lymph-sinus. *OP.* "Plug" of luteal tissue occupying site of follicular opening. *OO.* Oocyte. *TE.* Theca externa. *TE*[1]. Theca externa ingrowths, along which are theca-interna cells. × 34.

## Plate VII.

Fig. 13. Low-power view of section through the corpus luteum of Stage IV. In this case the "plug" or "bouchon" *OP*, marking the site of closure, takes the form of a circular cap with an overhanging margin, surmounting and continuous with the main body of the corpus luteum. *BV.* Blood-vessels. *TE.* Theca externa. *TE*[1]. Ingrowth of theca externa. × 34.

Fig. 14. Portion of central region of corpus luteum, Stage IV. *CF.* Chondriocontes. *BV.* Capillaries. *LC.* Luteal cells. *TE.* Interstitial connective tissue of theca externa. *TI.* Theca-interna cells. × 230.

PLATE VIII.

Fig. 15. Portion of corpus luteum, Stage V. *BV.* Capillary. *LC.* Luteal cell with vacuolated nucleus. *LC*[1]. Degenerate luteal cell. *TI.* Theca-interna cells. × 350.

Fig. 16. Portion of corpus luteum, Stage V. *BV.* Capillary. *LC.* Luteal cell. *TI.* Theca-interna cells. × 350.

PLATE IX.

Fig. 17. Low-power view of section through the corpus luteum of *Echidna*, Stage VI. *BV.* Blood-vessel or capillary. *LS.* Lymph-sinus. *OO.* Oocyte. × 34.

Figs. 18, Plate IX., & PLATE X. 19. High-power views of portions of the corpus luteum of *Echidna*, Stage VI. *BV.* Capillary. *CO.* Colloid droplet in luteal cell. *GS.* Granular degeneration sphere. *PH.* Polymorphonuclear leucocytes *PL.* Plasmosome. *TE* Interstitial connective tissue of theca externa. *V.* Vacuole. *VN.* Vacuolated nucleus. × 500.

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# 36. On some Larval Euphausiids from the Mediterranean in the Neighbourhood of Alexandria, Egypt, collected by Mr. F. S. Russell. By Marie V. Lebour, D.Sc., F.Z.S., Naturalist at the Marine Biological Laboratory, Plymouth.

[Received May 1, 1926: Read June 15, 1926.]

(Text-figures 1–4.)

The following notes on some larval euphausiids collected by Mr. F. S. Russell while working for the Fisheries Research Department of the Egyptian Government are supplementary to the paper on larval *Stylocheiron* (Lebour, 1926 *b*). All come from the same series of samples taken within a radius of ten miles from Alexandria. The fact that so many were obtained in this region seems to point to a general movement, for the purposes of spawning, from the open sea to nearer land. This has already been noticed in the case of *Meganyctiphanes norvegica* and *Thysanoessa inermis* (Lebour, 1924, 1925, 1926 *a*). It does not follow, however, that shallow water is necessary, for the deep water begins very close to the land in the neighbourhood of Alexandria, and it is probably a question of the larvæ obtaining more abundant food. In the case of *Stylocheiron* no larvæ were taken after May 1st at a temperature of 21°·75 C., and these were nearly adult, the young larvæ being obtained entirely in the early part of the year from January to March 1923, when the temperature was between 17°·8 C. and 18°·2 C. It is almost the same with the other larvæ described here, the bulk occurring from January to March, only a very few being present in April and May. Those occurring at the highest temperature of 26° C. were two early Furcilia stages of *Euphausia krohnii*. No euphausiids occurred in the samples taken after June 4th, when from July to August the temperature rose to 29° C.

At the end of the paper is a list of all the specimens found, exclusive of *Stylocheiron*, which are recorded in the previous paper (1926 *b*); and here similar data are given of date, capture, locality, depth, length of rope out, and temperature. The depth at which the net was fishing is probably in the region of a quarter the length of rope used.

Fourteen species of euphausiids are known to occur in the Mediterranean, and eight or nine different larvæ have been found in these samples. Of these, only two have not been identified, and these may belong to the same species, probably a *Euphausia*. The larvæ of two species of *Stylocheiron*—*S. suhmii* and *S. abbreviatum*—have already been described, and three

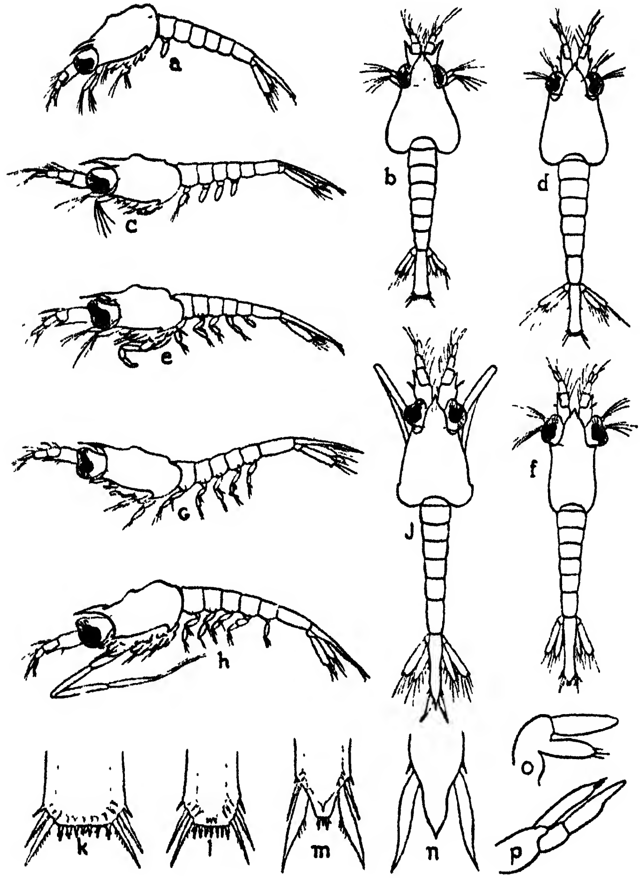
series of larvæ are described here—*Nematoscelis microps*, *Thyanopoda æqualis*, and some stages of *Euphausia krohnii*, part of which Sars (1885) has already described and figured. Besides these, a few larvæ of *Nyctiphanes couchii* and *Meganyctiphanes norvegica* were found, making, with the unidentified forms, a total of eight or nine species in this neighbourhood. The only adults seen belonged to *Stylocheiron suhmii*.

## *The Larvæ of* Nematoscelis microps *G. O. Sars.* (Text-fig. 1.)

It is curious that the only *Nematoscelis* larvæ known belong to *N. microps*, which must be an exceedingly abundant species. Hansen (1912) describes a few stages, and Sars (1885) also describes some under the name of *N. rostrata*, which is shown by Hansen to be synonymous with *N. microps*. The present material shows a fine series of larvæ from the second Furcilia to various Cyrtopia stages. The series shows a development of the pleopods similar to *Nyctiphanes* and *Meganyctiphanes*, the second pleopod being setose before the appearance of the fifth. Characteristic of the larva is its small size, sharp, leaf-like, elongated rostrum, very conspicuous dorsal hump to the carapace, which has a strong lateral denticle, and long second thoracic legs at an early stage, which, even in the sixth Furcilia, are easily recognizable doubled in under a covering skin.

The youngest stage found is presumably the second Furcilia, measuring 2·4 mm. in length, and having one pair of simple bud-like pleopods (text-fig. 1, *a*, *b*). The next seen has one pair of pleopods setose and three pairs simple, presumably the sixth Furcilia (text-fig. 1, *c*, *d*), measuring 2·7 mm. in length. These two stages correspond with the second and sixth Furcilia of *Nyctiphanes* and *Meganyctiphanes*, but it is conceivable that intermediate stages are skipped. It is striking that these stages, together with the tenth, seem to be dominant, as no intermediate stages were found, whilst these were abundant. Moreover, the sixth and tenth are the stages described by Hansen and Sars. In the sixth stage the long second thoracic legs can be seen doubled in. The next stage found, presumably the tenth, has four pairs of setose pleopods and one pair simple (text-fig. 1, *e*, *f*), measuring 2·7 mm. in length, the second thoracic legs free and fairly long. After this comes a stage which may be either the last Furcilia or the first Cyrtopia, with all the pleopods setose. It is here regarded as the last Furcilia (text-fig. 1, *g*), measuring 2·75 mm. in length. The antennæ have still two unjointed rami, but the setæ are almost gone and the whole organ very much diminished, so that they can be no longer used for swimming. The long thoracic legs are unfortunately broken. The stage here regarded as the first Cyrtopia (text-fig. 1, *h*) measures 3·2 mm. in length. It has a two-jointed flagellum to the antenna, and the second thoracic legs are fully formed, the bent joint reaching

Text-figure 1.




*Nematoscelis microps.*

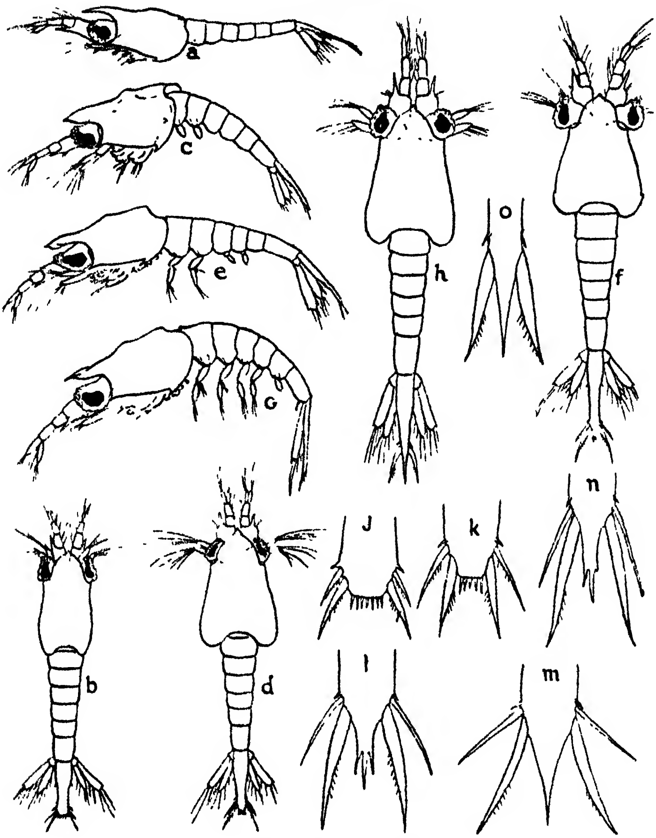
*a, b.* Second Furcilia, 2·4 mm. long, side and dorsal views. 21. 2. 23.
*c, d.* Sixth Furcilia, 2·7 mm. long, side and dorsal views. 21. 2. 23.
*e, f.* Tenth Furcilia, 2·7 mm. long, side and dorsal views. 13. 2. 23.
*g.* Last Furcilia, 2·75 mm. long. 13. 2. 23.
*h, j.* First Cyrtopia, 3·2 mm. long, side and dorsal views. 25. 1. 23.
*k.* Telson of second Furcilia.
*l.* Telson of sixth Furcilia.
*m.* Telson of tenth Furcilia.
*n.* Telson of last Furcilia.
*o.* Antenna of last Furcilia.
*p.* Antenna of first Cyrtopia.

nearly to the end of the antennules. There are a few later Cyrtopia stages present, but unfortunately the long legs are nearly all broken off. One adolescent stage with a pointed rostrum corresponds almost exactly with the figure of *Nematoscelis rostrata* of Sars (1885), which Hansen recognized as belonging to *N. microps*. The eyes of all these stages are in two parts, somewhat resembling those of *Stylocheiron*. The changes in the telson take place in the usual order. Seven terminal spines are present in the early Furcilia, the seven giving rise to five and sometimes to three. In the second Furcilia with one pair of simple pleopods there are seven giving rise to five, which in the specimen figured (text-fig. 1, *k*) are visible under the skin. This may, however, be abnormal, for in the sixth Furcilia with one pair of setose and three pairs of simple pleopods there are specimens with seven spines giving rise to three, which show under the skin. In the tenth Furcilia with four pairs of setose pleopods and one pair simple there are three terminal spines giving rise to one, with two pairs of long laterals in the last Furcilia, and in the first Cyrtopia the outer pair of long laterals have disappeared (text-fig. 1, *k*–*n*). The Cyrtopias are all fairly early stages until the adolescent stage mentioned above. Here we have an almost complete series of young stages—enough to identify the species through all its early life.

### *The Larvæ of* Thysanopoda æqualis *Hansen.*
(Text-fig. 2.)

Another series of larvæ in the Alexandria material almost certainly belongs to *Thysanopoda æqualis*. These have a certain resemblance to *Nematoscelis*, but differ in having no long leg and a blunter rostrum, although this is pointed and somewhat resembles that of *Nematoscelis*. The carapace is more massive, with less carination and a smaller dorsal knob placed not so far forward, and the whole animal is of a more clumsy build and larger in corresponding stages; moreover, the eyes are very characteristic, being of a peculiar oblong shape, with the lenses much raised, giving them a crenulated appearance. The development of the pleopods appears to take place in the same order as *Nematoscelis*, and there is a good series of larvæ in the samples. The first Furcilia (text-fig. 2. *a*, *b*), the earliest stage seen, measures 2·6 mm. in length. It has no pleopods, thus resembling *Nyctiphanes*, *Meganyctiphanes*, *Thysanoessa*, and *Stylocheiron*. It seems extremely likely that this stage without pleopods is a general one. The next stage present (text-fig. 2, *c*, *d*), measuring 2·9 mm. in length, is probably the third Furcilia having two pairs of simple pleopods. Then, apparently, several stages are absent, and the next seen, measuring 3·5 mm. (text-fig. 2, *e*, *f*), probably the seventh Furcilia, has two pairs of setose pleopods and two pairs simple. Thus in the development of the pleopods it agrees with *Nematoscelis*, *Nyctiphanes*, and *Meganyctiphanes*, and

Text-figure 2.




*Thysanopoda æqualis.*

*a, b.* First Furcilia, 2·6 mm. long, side and dorsal views. 13. 3. 23.
*c, d.* Third Furcilia, 2·9 mm. long, side and dorsal views. 13. 3. 23.
*e, f.* Seventh Furcilia, 3·5 mm. long, side and dorsal views. 5. 2. 23.
*g.* Tenth Furcilia, 3·7 mm. long. 5. 2. 23.
*h.* Last Furcilia, 3·8 mm. long. 5. 2. 23.
*j.* Telson of first Furcilia.
*k.* Telson of third Furcilia.
*l.* Telson of seventh Furcilia.
*m.* Telson of penultimate Furcilia.
*n.* Telson of tenth Furcilia.
*o.* Telson of last Furcilia.

differs from *Thysanoessa* and *Stylocheiron* (Lebour, 1926 *a*, *b*). The tenth Furcilia (text-fig. 2, *g*), measuring 3·7 mm. in length, has four pairs of setose pleopods and one pair simple, and finally

there are two Furcilia stages with all the pleopods setose and several Cyrtopia stages measuring up to 5·5 mm. in length. The last stages seem to be recognizable as *Thysanopoda æqualis* by the antennules, although these are by no means fully developed. The telson has a tendency towards quick development, and although the first Furcilia has the usual seven terminal spines, the third has only five, the seventh and the tenth have three, the penultimate Furcilia has one with two pairs of laterals, and the last Furcilia and all the Cyrtopia stages have only one pair of laterals (text-fig. 2, *j*, *o*).

*Thysanopoda æqualis* in its larval stages is very unlike the description given by Sars (1885) of *T. tricuspidata*, but the eyes are in two distinct parts in both, although differently situated, and the pleopods apparently develop similarly, there being a first Furcilia with no pleopods at all.

### *The Larvæ of* Euphausia krohnii *Brandt*.
(Text-figs. 3, 4, *a–d*.)

At present the only species of *Euphausia* whose development is known in more than one or two stages is *E. pellucida*, described by Sars (1885). This has been shown by Hansen to be a mixture of two or three species belonging to the *krohnii* group. Most of those figured are almost certainly the younger stages of *E. krohnii*. Sars described them from the second Calyptopis up to an early Cyrtopia, but the Cyrtopia must belong to another species, for in the Alexandria samples there is a series of larvæ from metanauplius to Cyrtopia, and this last still retains the fringed rostrum characteristic of all the younger stages which is absent in the Cyrtopia figured by Sars.

The metanauplius and first Calyptopis are described here for the first time. Sars describes the second and seventh Furcilia, having one pair of simple pleopods, and one pair setose, with four pairs simple respectively. Curiously enough, no stages between these two have been found in the Alexandria samples, although many specimens of both these stages occurred. Possibly this is again a case of jumping over several stages, which was suggested above for *Nematoscelis*. Mr. Elmhirst, of Millport, has given me many instances of skipping stages in *Meganyctiphanes norvegica*, although this is apparently abnormal for that species.

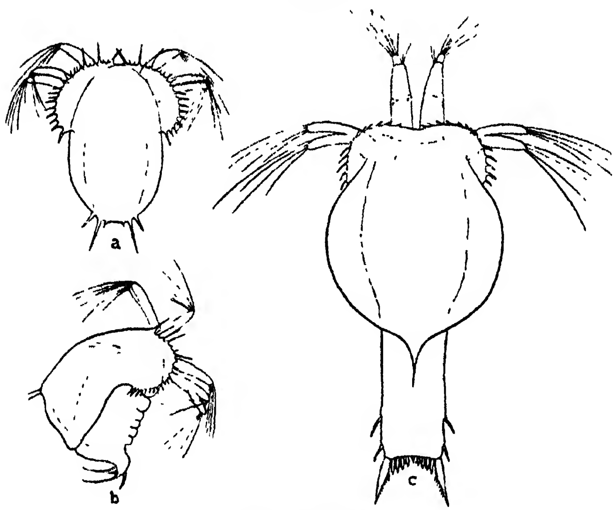
There is now a series of larvæ of *E. krohnii* known from metanauplius to Cyrtopia, showing that it develops somewhat differently from *Nyctiphanes*, *Meganyctiphanes*, *Nematoscelis*, and *Thysanopoda* with regard to the pleopods. Other *Euphausia* species, however (Tattersall, 1925), go through a stage with one pair of pleopods setose and three simple, so that it may be presumed that the series in *Euphausia* develops normally in this way, but, unlike the *Nyctiphanes* group (including those genera cited above), the Furcilia following the stage having one pleopod setose and three simple has the fifth pleopod simple before the

second is setose, instead of having two setose before the fifth has formed, thus also differing from *Thysanoessa*, in which there is a stage with all pleopods simple before any are setose.

The metanauplius of *Euphausia krohnii* (text-fig. 3, *a*, *b*) has the typical fringed rostrum, broad and bordered with spines. The length from the anterior end of the rostrum to the posterior end of the telson is 0·4 mm. The body is bent almost at a right angle, and there are two setæ projecting from the dorsal angle almost at the centre of the body. The telson is armed with six spines.

The first Calyptopis (text-fig. 3, *c*) measures 0·88 mm. in

Text-figure 3.

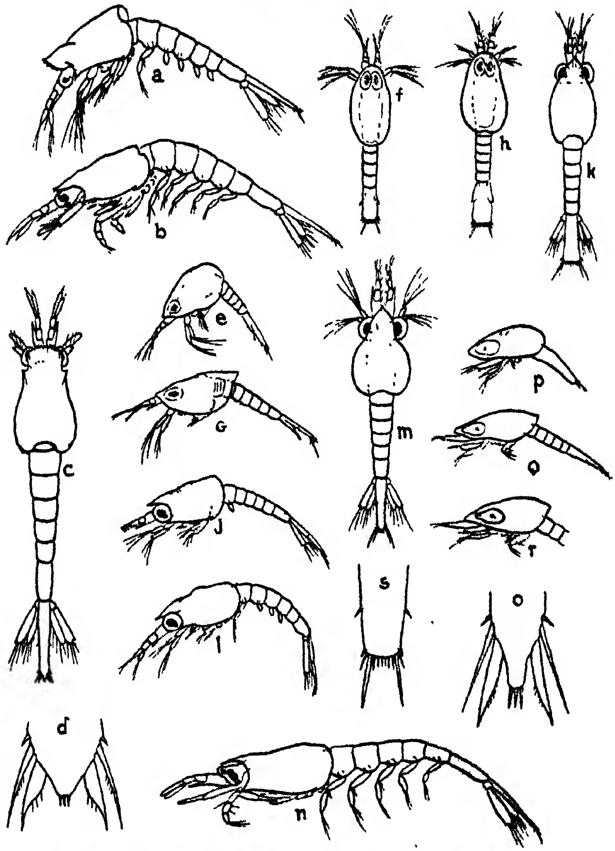



*Euphausia krohnii.*

*a*, *b*. Metanauplius, 0·4 mm. long, dorsal and side views. 23.1.23.
*c*. First Calyptopis, 0·88 mm. long. 23.1.23.

length, the rostrum now being much smaller in proportion to the rest of the carapace. There is a long spine at the extreme posterior end of the carapace which continues through several larval stages. The telson is armed with the usual number of spines, one lateral pair at the sides, one lateral pair just above the posterior angle, two pairs of posterior laterals, only the outer pair of which is long in this stage, and seven terminal spines. In the second and third Calyptopis, which are similar to Sars's figure, the inner laterals are long; the rostrum is like the first, with a fringed border which, in the earliest Furcilia seen (here regarded as the second), still partly covers the eyes. Indeed, the

Text-figure 4.




*Euphausia krohnii*, *Euphausia* sp. (?), and *Stylocheiron suhmii*.

*a–d*. *Euphausia krohnii*.

*a*. Seventh Furcilia, 8 mm. long. 1. 5. 23.
*b*, *c*. First Cyrtopia, 3·7 mm. long, side and dorsal views. 21. 3. 23.
*d*. Telson of first Cyrtopia.

*e–m*. *Euphausia* sp. (?).

*e*, *f*. Second Calyptopis, 1·6 mm. long, side and dorsal views. 23. 1. 23.
*g*, *h*. Third Calyptopis, 1·8 mm. long, side and dorsal views. 23. 1. 23.
*j*, *k*. Second Furcilia, 2 mm. long, side and dorsal views. 23. 1. 23.
*l*, *m*. Sixth Furcilia, 2·3 mm. long, side and dorsal views. 23. 1. 23.
*n*. Cyrtopia (first or second) of *Euphausia* sp., 3·84 mm. long. 1. 5. 23.
*o*. Telson of same.

*p–s*. *Stylocheiron suhmii* G. O. Sars.

*p*. First Calyptopis, 1·28 mm. long. 23. 1. 23.
*q*. Second Calyptopis, 1·76 mm. long. 23. 1. 23.
*r*. Third Calyptopis, broken. 23. 1. 23.
*s*. Telson of second Calyptopis.

large fringed rostrum extends partly over the eyes, even in the early Cyrtopia. The second Furcilia with one pair of simple pleopods measures 2·4 mm. in length, and still has the long posterior spine on the carapace. It is similar to Sars's first Furcilia, which he describes and figures. The next stage seen is also described and figured by Sars (as the second Furcilia), having one pair of setose and four pairs of simple pleopods. This is such a characteristic stage, and, so far as is at present known, occurring only in this *Euphausia*, that it is of great importance, and is re-figured here (text-fig. 4, *a*). This appears to be the seventh Furcilia, and is one of the dominant stages constantly occurring. No stages intermediate between this and the second Furcilia have been found, neither have later stages been found between this and the last Furcilia. The seventh Furcilia measures 3 mm. in length, and has lost the long posterior spine of the carapace. The Furcilia with all pleopods setose is presumably the last. It measures 3·3 mm. in length, and corresponds with Sars's last Furcilia. A Cyrtopia, measuring 3·7 mm., probably the first (text-fig. 4, *b*, *c*, *d*), has still a fringed rostrum, the antennæ having a well-marked flagellum and scale. This differs from Sars's first Cyrtopia in having the fringed rostrum, the two being almost certainly different species.

There is another euphausiid larva in the samples, probably a *Euphausia* (text-fig. 4, *e–m*). This is a very small species. The second and third Calyptopis and the second and sixth Furcilia are present. The Calyptopis stages, measuring 1·6 mm. and 1·8 mm. in length respectively, have a simple oval carapace, the telson bearing seven terminal spines. At the posterior end in the third stage the carapace seems to be drawn out slightly when viewed sideways, giving it the appearance of a spine; but this disappears in the dorsal view, and the carapace is indented posteriorly in the second Furcilia, which measures 2 mm. in length and has one pair of simple pleopods. The eyes are small and round, and the carapace pointed anteriorly in a leaf-like rostrum which is quite unlike that of *Euphausia krohnii*. The sixth Furcilia measures 2·3 mm. in length and has one pair of setose and three pairs of simple pleopods, the rostrum being rather more elongated. At the side of the carapace in these two Furcilia stages there is a fairly strong lateral denticle.

A Cyrtopia (first or second) which may belong to this species is almost certainly a species of *Euphausia* (text-fig. 4, *n*, *o*). This measures 3·84 mm. in length and has a leaf-like rostrum very much like the earlier larvæ described above. The antennæ have a well-formed flagellum and scale. This stage resembles closely the first Cyrtopia of *E. krohnii* described above, differing in its rostrum and general figure. The telson is similar in both, with three terminal spines.

Three Calyptopis stages of what is almost certainly *Stylocheiron suhmii* occurred (text-fig. 4, *p–s*). These were found after the

paper on the other larval stages of this species was in the press (Lebour, 1926 *b*). The last Calyptopis was, unfortunately, incomplete, but showed the rudiments of the pear-shaped eyes with its few anterior lenses so characteristic of this species, and the telson of the first and second stages had only six terminal spines. *S. suhmii* is so far the only euphausiid known which has only six in the second Calyptopis, although *Thysanoessa inermis* has only six in the first Calyptopis but seven in the second. These Calyptopis stages of *S. suhmii* are somewhat chrysalis-like in form, with the joints of the abdomen unusually smooth and flattened and the carapace closely fitting, so that, when extended, the whole outline is smooth. The first Calyptopis measures 1·28 mm. in length, the second 1·76 mm.; the third has the end of the abdomen missing.

From these notes it is seen that a large number of larval euphausiids are contained in these samples which help to throw light on the general development of the group. All develop in a similar way to a certain extent, but there are important differences, some of which appear to be generic (*e. g.* in the order of development of the pleopods), others specific (*e. g.* in the number of terminal spines on the telson or the presence or absence of lateral spines on the carapace).

A survey of all euphausiid larvæ known, with some notes on their general development, is now written and ready for publication.

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## *Data showing the Catches of Larval Euphausiids in the Samples.*

### 1923.

Jan. 23rd. Lat. 31° 11′ 30″ N., Long. 29° 48′ 20″ E., 10.45 A.M., depth 17 f., length of rope out 20 f. ***Nematoscelis microps***: one 2nd Furcilia, two 6th Furcilia, two 10th Furcilia. ***Thysanopoda æqualis***: one 3rd Furcilia, two 7th Furcilia, five Cyrtopia. ***Euphausia krohnii***: two metanauplii, twenty-four 1st Calyptopis, thirty-one 2nd Calyptopis, eleven 3rd Calyptopis, six 2nd Furcilia. ***Euphausia*** sp.: one 2nd Calyptopis, two 1st Furcilia.

Jan. 25th. Lat. 31° 9′ 20″ N., Long. 29° 41′ 00″ E., 9 A.M., depth 17 f., length of rope out 20 f., surface-temperature 17·8° C. ***Nematoscelis microps***: one 10th Furcilia, two Cyrtopia. ***Thysanopoda æqualis***: one 10th Furcilia, two Cyrtopia. ***Euphausia krohnii***: two 2nd Calyptopis, two 3rd Calyptopis.

Feb. 5th. Lat. 31° 19′ 40″ N., Long. 29° 41′ 00″ E., 2 P.M., depth over 100 f., length of rope out 60 f., surface-temperature 18·1° C. ***Thysanopoda æqualis***: two 7th Furcilia, seven 10th Furcilia, seven last Furcilia, eighty-three Cyrtopia.

Feb. 21st. Lat. 31° 12′ 30″ N., Long. 29° 47′ 00″ E., 3.45 P.M., depth 23 f., length of rope out 50 f., surface-temperature 18·1° C. ***Thysanopoda æqualis***: five Cyrtopia. —Lat. 31° 11′ 30″ N., Long. 29° 45′ 20″ E., 11.10 A.M., depth 20 f., length of rope out 30 f., surface-temperature 17·5° C. ***Nematoscelis microps***: one 2nd Furcilia, one 6th Furcilia. ***Euphausia krohnii***: twenty-six 2nd Calyptopis, fifty-two 3rd Calyptopis, twenty-eight 2nd Furcilia, six 6th Furcilia. ***Euphausia*** sp.: one last Calyptopis.

Mar. 12th. Lat. 31° 16′ 45″ N., Long. 29° 51′ 30″ E., 11.4 A.M., depth 30 f., length of rope out 50 f., surface-temperature 16·75° C. ***Nematoscelis microps***: five 2nd Furcilia, five 6th Furcilia, one 10th Furcilia, one last Furcilia, one Cyrtopia. ***Thysanopoda æqualis***: five 3rd Furcilia, eight 7th Furcilia, four last Furcilia, three Cyrtopia. ***Euphausia krohnii***: one 1st Calyptopis, one last Calyptopis, twenty-five 2nd Calyptopis, thirty-six 3rd Calyptopis, thirty-one 2nd Furcilia, five 6th Furcilia. ***Euphausia*** sp.: one 1st Calyptopis. ***Nyctiphanes couchii***: one 2nd Calyptopis. ***Meganyctiphanes norvegica***: two 1st Furcilia.

Mar. 13th. Lat. 31° 14′ 30″ N., Long. 29° 38′ 40″ E., 9.45 A.M., depth 29 f., length of rope out 50 f., surface-temperature 17·4° C. ***Nematoscelis microps***: five 2nd Furcilia, five 6th Furcilia, two 10th Furcilia. ***Thysanopoda æqualis***: two 1st Furcilia, five 3rd Furcilia, ten 7th Furcilia, five Cyrtopia. ***Euphausia krohnii***: four 2nd Calyptopis, fourteen 3rd Calyptopis, ten 2nd Furcilia, two 6th Furcilia.—Lat. 31° 8′ 00″ N., Long. 29° 40′ 50″ E., 11.44 A.M., depth 29 f., length of rope out 15 f., surface-temperature 17·4° C. ***Nematoscelis microps***: one 2nd Furcilia, two 6th Furcilia. ***Euphausia*** sp.: one 2nd Calyptopis. ***Nyctiphanes couchii***: one last Furcilia.—Lat. 31° 8′ 00″ N., Long. 29° 40′ 50″ E., depth 14 f., length of rope out 37 f., surface-temperature 17·5° C. ***Thysanopoda æqualis***: two 3rd Furcilia. ***Nyctiphanes couchii***: one 1st Furcilia.

April 10th. Lat. 31° 14′ 15″ N., Long. 29° 51′ 15″ E., 10 A.M., depth 25 f., length of rope out 50 f., surface-temperature 18·2° C. ***Thysanopoda æqualis***: one 7th Furcilia, two Cyrtopia.

May 1st. Lat. 31° 18′ 30″ N., Long. 29° 49′ 30″ E., 10.35 A.M., depth 37 f., length of rope out 50 f., surface-temperature 21·75° C. *Nematoscelis microps*: one 6th Furcilia, one Cyrtopia. *Thysanopoda æqualis*: three 7th Furcilia, two 10th Furcilia, two last Furcilia, five Cyrtopia. *Euphausia krohnii*: one 2nd Furcilia, one 6th Furcilia. *Euphausia* sp.: one Cyrtopia (possibly a different species).—Lat. 31° 15′ 30″ N., Long. 29° 50′ 15″ E., 9.17 A.M., depth 25 f., length of rope out 25 f., surface-temperature 21·3° C. *Nematoscelis microps*: one 6th Furcilia.

June 4th. Lat. 31° 13′ 45″ N., Long. 29° 46′ 00″ E., 11.37 A.M., depth 28 f., length of rope out 40 f., surface-temperature 26° C. *Euphausia krohnii*: two 2nd Furcilia.


HYBRID ANURA.

## 37. Note on the Occurrence of Hybrid Anura at Lobatsi, Bechuanaland Protectorate. By J. H. Power, F.Z.S.

[Received April 13, 1926: Read June 1, 1926.]

(Plate II.*)

That different species and even genera of Anura pair is a well-known fact, hence, it is not surprising that *Bufo carens* and *Bufo regularis* were found pairing at Lobatsi; a male *B. regularis* with a female *B. carens* and vice versa.

These two toads are, however, so widely separated morphologically that one is naturally very interested in the result of such a combination.

Unfortunately the writer was unable to secure the eggs of such pairs owing to the great numbers of toads breeding in the same pool. Young and half-grown specimens were extensively collected, and these yielded two which, in the writer's opinion, are hybrids. (*a*) and (*c*) on the accompanying Plate have the following characteristics of *B. carens*.

Flank marked off distinctly from the dorsal surface by a glandular dorso-lateral fold and by contrasting colours. The tarsal fold very well developed and occupying the whole length of the tarsus. The fingers and toes slender, with the exception of the third finger of the left hand in (*a*) which is very short and thick. The fourth finger of the right hand and the third of the left are short and thick in (*c*). The first finger is the longest in both.

Both specimens resemble *B. regularis* in the presence of distinct parotoid glands; these are rather flat in (*c*) but quite prominent in (*a*).

(*a*) seems to have more of the characteristics of *B. regularis*, while (*c*) is more like *B. carens*. The skin in both specimens is comparatively smooth; the dorsal surface has scattered and very flat tubercles. The snout in both cases is typical of juvenile specimens of *B. carens*. A specimen of *B. carens* (*a*) about the same age and a specimen of *B. regularis* (*b*) slightly younger are shown for comparison.

The presence of a thin vertebral line and scarlet patches in the axillary and inguinal regions in (*a*), also at the posterior part of the body covered by the legs when at rest, raises the question as to whether *Bufo tuberculosus* Boc. may not be a cross between *B. regularis* and *B. carens*. All three species occur at Lobatsi, *B. tuberculosus* being the least plentiful and *B. carens* the most plentiful.

* For explanation of the Plate see p. 778.

## EXPLANATION OF THE PLATE.

A. Hybrid with prominent parotoids. (Natural size.)
B. *Bufo regularis* for comparison. (Natural size.)
C. Hybrid with flattened parotoids. (Natural size.)
D. *Bufo carens* for comparison. (Natural size.)

The above are all from Lobatsi, B.P., and are about two-thirds grown except (*b*), which is only half grown.

# 38. On Marine Chironomidæ (Diptera); with Descriptions of a New Genus and four New Species from Samoa. By F. W. Edwards* (British Museum, Natural History).

[Received April 27, 1926: Read June 15, 1926.]

(Text-figures 1–8.)

Contents.



## A. Marine Chironomidæ: a Review of Present Knowledge.

Flies of the family Chironomidæ are amongst the most ubiquitous of insects, and their larvæ are to be found in almost every collection of water, large or small, no matter where situated and no matter how saline its composition. The existence of Chironomid larvæ in the sea has been known ever since 1830, when Johnston first described his famous *Campontia eruciformis*; since that date quite a number of such species have been reported from various parts of the world. Before proceeding to describe the remarkable insects found by P. A. Buxton in Samoa, it will be useful to summarize our knowledge of sea-breeding Chironomidæ in other parts of the world. In this connection we need only concern ourselves with those which breed in freely-moving sea water. In addition to these, there are many others which are more or less definitely addicted to brackish or salt water, either near the coast or in inland salt areas. A number of these have been discussed by Thienemann (29) in his paper on salt-water Chironomidæ. The biological

* Communicated by Dr. P. A. Buxton, F.Z.S.

conditions of isolated and stagnant collections of salt water, however, are quite different from those obtaining in the sea itself, and many larvæ which are able to stand any degree of salinity in still water are never found in water which is open to tidal action. This is especially noticeable in the case of the coastal mosquitoes, and it appears to be true in general of Chironomidæ also, although it is not improbable that some of the mud-inhabiting forms may be found to occur in both stagnant and tidal areas. At present few data are available with regard to such estuarine Chironomidæ as may fall into this category.

With the possible exception of some of the mud-inhabiting forms just referred to, none of the species which are truly marine are found breeding anywhere except in the sea. It is remarkable that none of them, so far as known, show any noteworthy modifications in either the larval or the pupal stage, except that the blood-gills of the larva and the prothoracic respiratory horn of the pupa are often reduced or absent. In many cases also, the adults have undergone hardly any change; but, on the other hand, many of them are more or less profoundly modified: first, by the loss of the secondary sexual characters of the male, the antennæ coming to resemble those of the female; and, secondly, by the partial or complete loss of the wings and halteres. We will briefly discuss the various forms known in these two categories.

## 1. Unmodified Species.

Practically all the species known to fall into this category belong to the tribe Orthocladiariæ in the sense of Kieffer. Almost the only exceptions are some species of *Culicoides* (subfamily Ceratopogoninæ) which have been recorded as breeding in mangrove swamps; such are *Culicoides marium* Lutz of Brazil, and *C. maculithorax* Williston of South and Central America and the West Indies. The remaining species are mentioned below; I have included two British forms which have not hitherto been recorded. The genera represented are all widely spread, and most of their members breed in fresh water, a few even being terrestrial.

*Orthocladius oceanicus* (Packard) (**24**).—Larvæ were dredged from a depth of 30 fathoms in Salem Harbour, U.S.A. Johannsen (**12**) and Thienemann (**29**) have pointed out that the species belongs to the *Orthocladius* group, but its exact position is uncertain; it may perhaps be a *Psectrocladius* or a *Trichocladius*; if the latter, it is not impossible that it may be identical with the North European *T. variabilis* Staeg.

*Orthocladius* (*Dactylocladius*) *kervillei* Kieffer (**17**).—Reared by Gadeau de Kerville from larvæ found in a disused oyster-bed on the Normandy coast. The species has not been recorded since, and it seems doubtful if it is a truly marine form. Larvæ

of a species of *Chironomus* were found associated with it, and have been described by Potthast (**25**).

*Orthocladius* (*Dactylocladius*) *mercieri* Kieffer and *Camptocladius* (*Phænocladius*) *rupicola* Kieffer (in Mercier, **23 a**).—Captured on a rock between tide-marks on the Calvados coast. Though Mercier classes both species as truly marine, he does not state whether the early stages were obtained.

*Trichocladius variabilis* (Staeger).—Having examined the types of Staeger's *Chironomus variabilis*, I find that this species belongs to *Trichocladius*, and is probably identical with Alverdes's *T. marinus* and Kieffer's *T. halophilus*. It is widely spread in North Europe, and I have also seen specimens from the Faeroe Islands and Iceland which scarcely differ. It was first recorded as a sea-breeding species by Alverdes (**1**), who found larvæ in water of varying degrees of salinity and various depths in the Norwegian fjords near Bergen, among roots of seaweed. Thienemann (**24**, **30**) records it from Kiel, the Swedish west coast (Kullen), and also from inland salt areas of Westphalia, stating that this species is one of the few which occur in salt water both inland and in the sea. Whether the insects from Westphalia are the same species is perhaps open to question; there are certainly several very closely-allied but apparently distinct forms which will breed in brackish or even quite fresh water, one of these being common on muddy shores in Britain. *T. variabilis* has also been found breeding in the sea in Scotland; the larvæ are said by Mr. R. Elmhirst to occur frequently among *Enteromorpha intestinalis*, being generally found inside the hollow fronds. These specimens were recorded by Elmhirst (**9**) as *Orthocladius sordidellus* Zett., but I find on examining the material that the determination was incorrect.

*Camptocladius thalassophilus* Goet.—This was found by Bequaert and Goetghebuer (**3**) on the mole at Zeebrugge, the males hovering in the air and the females running over seaweed and rocks exposed at low tide. Mating was observed, and it is of interest to note that, instead of the female flying into the swarm of males (as usually happens), males now and again left the swarm and pounced on females as they sat on the rocks. It looks as though we may have here the first sign of the commencement of degeneration in the female. Larvæ were not found, but the authors were convinced from the habits of the adults that they must breed in the sea. This view derives strong support from the fact that the species has since been found in Britain under similar conditions. The late W. Evans recorded finding the males flying low over rock-pools near Edinburgh, and I have myself seen them on the coasts of North Devon, South Hampshire, and the island of Arran.

ORTHOCLADIUS (DACTYLOCLADIUS) BREVIFURCATUS, sp. n. (Text-fig. 1, *a* and *c*.)

♂. Body all black; pleural membrane, palpi, legs, and halteres dark brownish; wings milky-white.

Antennæ with the last segment a little longer than the previous 12 together; tip pubescent; plumes moderately dense. Palpi of normal structure. Thorax without pruinescence, mesonotum somewhat shining. Abdomen with a moderate amount of dark hair. Hypopygium (text-fig. 1, *a*) with a rather short, sharp, bare dorsal point; side-pieces with small rounded tubercular lobe beyond the middle; claspers blunt-ended, with a small apical lobe which in dorsal view covers the short spine. Tibiæ and tarsi with rather long hairs, the longest about three times as long as the diameter of the segment bearing them. Empodium about as long as the claws. Wings (text-fig. 1, *c*) with a slight brown tinge by transmitted light; surface quite bare. Costa not extending beyond tip of radius, and ending at about five-sixths of the wing-length, just above the tip of *Cu* 1. *R* 2+3 ending well beyond the middle point between the tip of *R* 1 and that of *R* 4+5. *M* ending at tip of wing. Cubital fork very short, the distance of its base from *r–m* being greater than the length of its lower branch. *Cu* 2 quite straight. About half-way between *r–m* and *fCu* a slight fold in the wing runs parallel to *Cu* 2.

Length of body, about 1·8 mm.; wing, 1·3 mm.

15 ♂ (co-types), Swanage, Dorset. 6. ix. 1906, "in great numbers hovering in flocks over boulders on the sea-shore" (*Lt.-Col. Yerbury*). Also 4 ♂, Porlock Weir, Somerset, 10. vi. 1922, flying on shore between tide-marks (*F. W. Edwards*).

This small black species at first sight resembles *Camptocladius thalassophilus*, but the legs are darker and the venation is quite different.

Trichocladius fucicola sp. n. (Text-fig. 1, *b*.)

♂. Body blackish; palpi, legs, and sometimes the pleural membrane brown; wings greyish-white, anterior veins hardly darkened; halteres pale yellowish.

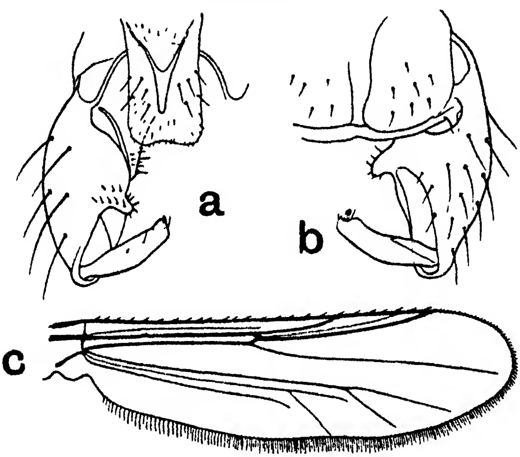
Antennæ rather shorter than usual, the plumes not very dense though quite well developed; last segment about 0·6 times as long as the preceding 12 together, these mostly about as broad as long, one or two at the base rather shorter. Palpi of normal structure, moderately long. Eyes densely hairy. Thorax usually with slight pruinescence, mesonotum slightly shining. Abdomen dull, with dark hair. Hypopygium without dorsal point: side-pieces with prominent basal lobe; claspers scarcely lobed at tip, with very stout blunt spine. Legs short-haired. First segment of front tarsi about two-thirds as long as the tibia; fourth and fifth tarsal segments about equal in length. Empodium longer than the claws. Wings with very slight brown tinge by transmitted light; surface bare. Anal lobe moderately produced. Costa extending slightly beyond tip of *R* 4+5 and ending well beyond the level of the tip of *Cu* 1; *R* 2+3 ending much nearer to *R* 1 than to *R* 4+5; *r–m* nearly vertical and somewhat darkened; *fCu* distinctly beyond *r–m*.

♀. Head blackish, slightly shining. Thorax mainly blackish, but shoulders obscurely ochreous, and the mesonotal stripes rather indistinctly separate. Antennæ 7-segmented; 2 somewhat constricted before the middle; 3–6 shortly oval with short slender sense-bristles and rather short verticils; 7 not quite as long as 4–6 together, without verticil, but with about a dozen curved sense-bristles arranged in three or four rows. Legs and wings as in the ♂.

Length of body, ♂ 3 mm., ♀ 2–2·5 mm.; wing, 2 mm.

5 ♂, 1 ♀, Porthcawl, Glamorganshire, 13. vii. 1906, "taken hovering in the air over seaweed-covered rocks near low-water line" (*Lt.-Col. Yerbury*); also 3 ♂ (including type), Bucks Mills,

Text-figure 1.




Hypopygium (*a*) and wing (*c*) of *Orthocladius brevifurcatus*, sp. n.
Hypopygium (*b*) of *Trichocladius fucicola*, sp. n.

N. Devon, 18. vi. 1922, flying on shore between tide-marks (*F. W. Edwards*); and 5 ♂, 1 ♀, Brodick, Arran, N.B., 22–25. v. 1919 (*F. W. Edwards*).

This is probably the species recorded by Elmhirst (**9**) as occurring in the Clyde area, "chiefly amongst *Polysiphonia fastigiata*, but also amongst *Zostera* and other weeds, at all tidal levels." Specimens sent me by Mr. Elmhirst appeared to agree with the types, but as they had lost their antennæ the identity is not quite certain. The most striking character of the species is the relatively short terminal segment of the male antennæ.

## 2. Modified Species.

**Of greater interest than the forms just discussed are those which show some modification in the adult in connection with**

their changed habitat. All of these are purely marine, the adults being found only on rocks and weed exposed at the lowest tides. Like the more normal species already referred to, all of them have a well-developed hairy empodium, which is believed to assist its possessor in running or skating over the surface of water; in some, such as *Paraclunio*, the empodium is unusually large and thickly branched. The reduction of the wings, first in the female and then also in the male, is a phenomenon which occurs in a number of other littoral flies

All these marine forms have been placed by Kieffer (**19**) in his subfamily Clunioninæ, the main if not the sole diagnostic character of which is the absence of a comb on the four posterior tibiæ. That the use of this character for defining a subfamily leads to an artificial grouping of genera seems fairly evident. The curious lacustrine genus *Corynocera*, also placed in Clunioninæ by Kieffer in 1913, has the long front tarsi and rigidly extended male claspers of the *Chironomus* group, and in the writer's opinion is to be regarded as a remarkably specialized form of *Chironomus*. Probably the same is true of the Indian genus *Nepalia*, but most of the remaining genera of Clunioninæ have the first front tarsal segment shorter than the tibia and the male claspers articulated and infolded in repose, in both these respects agreeing with the *Orthocladius* group of genera. They nevertheless show considerable variation in structural details, which almost certainly indicates a multiple origin from different branches of the *Orthocladius* group. This conclusion, based on adult morphology, has also been arrived at by Thienemann (**30**) from a study of the larvæ.

Reduction of the wings occurs in a number of Chironomidæ, and is associated with various conditions of life. Apart from the marine forms under discussion, it occurs in several non-marine insular forms, and there is one case on record (the genus *Cataliptus*, described by Bezzi from North Africa) of a cave-dwelling species having lost its wings. Some of these degraded species, though placed in separate genera, have departed but little in essential structures from their parent species. Thus the two arctic species included by Holmgren in his genus *Smittia* appear to me from a study of the types to be subapterous species of *Camptocladius* (*S. brevipennis*) and *Metriocnemus* (*S. longipennis*), and the antarctic *Belgica*, to judge from the description, might well be simply a subapterous *Orthocladius*.

Most if not all of the species with reduced wings also have similar antennæ in the two sexes, those of the male having come to resemble those of the female by the loss of the "plumes" and reduction in the number of segments. That this should be so is not at all surprising when one remembers that the plumose male antennæ of the normal Chironomid are connected with their aerial mating habits. A change of the mating area from the air to the ground might well initiate a change in the secondary sexual characters of the males.

The adults of the marine species have been observed skating over the surface of the water as well as running rapidly over rocks, and the winged forms take short flights close to the water's surface. Some are also able to stand submergence, one species (*Clunio adriaticus*) having been found below the sea among *Mytilus* colonies. This, however, is exceptional; the fact that newly-emerged adults appear shortly after the tide has receded and accomplish both mating and oviposition before the return of the water strongly suggests that normally they live only these few hours. According to Chevrel, both *Clunio* and *Thalassomyia* live in zones which are uncovered only by the lowest tides, and are therefore dependent on the lunar cycle.

### Clunio Hal.

Apart from the still somewhat problematical *Campontia*, this was the first marine Chironomid to be recorded, Haliday having described the male in 1855, although it was not till 1894 that the female and larva were discovered independently by Chevrel (**6**) and Carpenter (**5**). A full historical summary of our knowledge of the genus up to 1913 has been given by Bezzi (**4**), and some further details regarding the larval and pupal anatomy have been furnished by Goetghebuer (**10**) and Thienemann (**29**, **30**). The last-named author considers that the larva shows affinity with the *Orthocladius* group, which it resembles in most respects, differing chiefly in the arrangement of the spines on the posterior suckers, and in having only a single hair on each dorsal tubercle of the pre anal segment, this last feature distinguishing it from most other Chironomid larvæ. The pupa also is not unlike that of *Orthocladius*. It should be noted that the larva described by Goetghebuer (**10**) as that of *C. marinus* does not belong to this genus: it may perhaps be that of *Camptocladius thalassophilus*.

The flies are remarkable for the great disparity of the sexes, the male having small but well-developed wings with a fairly normal venation, whereas the female lacks both wings and halteres. The male genitalia are also enormously enlarged. The female has short but normal legs. In both sexes each tibia has a single small bare spur; the fourth tarsal segment is not cordiform, nor is the fifth lobed at the tip; the claws are normal and the empodium is quite large; the front tarsi are short. The antennæ (11-segmented in the ♂, 7-segmented in the ♀) are peculiar in having the third segment elongate and cylindrical, and also in being nearly bare.

Three or four species have been described, all from European coasts, but the characters given for separating them are unsatisfactory. I am of opinion that *C. bicolor* Kieff. is identical with *C. marinus* Hal.: the supposed differences seem to be either non-existent or to be due to different methods of preservation, for Irish specimens I have examined agree in the main with

Kieffer's description. This species is known from European coasts from France and Ireland to Denmark. The Mediterranean forms (*C. adriaticus* Schin. and *C. balearicus* Bezzi) are also probably specifically identical, but appear distinct from *C. marinus* on account of their uniform light colour and small differences in the antennæ and hind tarsi.

THALASSOMYIA Schin.

This genus was erected by Schiner in 1856 for a marine species, adults of which were found on rocks and seaweed at low water near Trieste. Subsequently other species which were found breeding in rapid rivers were added to the genus by Tömösvary and Johannsen. Kieffer has rightly considered, however, that these river-breeding species are not congeneric with the marine *T. frauenfeldi*, and has referred them to his genus *Cardiocladius*. On the other hand, I have shown in a recent note that Chevrel's *Scopelodromus isemerinus* is the same insect as *Thalassomyia frauenfeldi*. Judging from the description, this appears to be the case also with *Scopelodromus canariensis*, described by Santos Abreu (27) in 1918. Up to the present, therefore, only one species of this genus is known; it occurs on the coasts of England, France, Belgium and Italy, and doubtless other European countries, as well as in the Canary Islands. There is also in the British Museum a female from Montevideo, Uruguay (*P. de la Garde*), which appears to belong to *T. frauenfeldi*. If so, this species has an extremely wide distribution, and may perhaps have been spread by shipping; assuming the larvæ and pupæ to be capable of maintaining their existence on the submerged part of the hull, the entry of the ship into dry dock would no doubt provide the necessary stimulus for the emergence of the adults. The sexes are similar, the wings being well developed, normal, with a venation like *Chironomus*. The chief features diagnostic of the genus are to be found in the tarsi: the fourth segment is short and cordiform; fifth normal, not trilobed; empodium large and hairy. The legs are long; femora thickened towards the base, especially the front pair; tibiæ with well-developed spurs, one on the front legs, two on the posterior pairs. The differences from *Clunio* are very considerable, but it seems probable that the genera are related.

The larvæ have been described in some detail by Chevrel (7), but not sufficiently to give any precise data on the relationships of the genus; they appear similar to *Orthocladius*, and are stated to occur among seaweeds and barnacles.

Recently a peculiar Chironomid has been described from the Galapagos Is. by C. W. Johnson (13) as *Galapagomyia longipes*. The description is inadequate and the figure of the wing is obviously inaccurate (it shows a quite impossible venation), nor are the habits noted, but from the data given it appears to me highly probable that it will prove to be a *Thalassomyia*. If so, it further extends the known range of the genus to a remarkable

extent, and there is little doubt that it will eventually be found to be cosmopolitan, like many of the terrestrial and freshwater genera of Chironomidæ.

There is in the British Museum a specimen of an unrecorded species of this genus from East Africa. It resembles *T. frauenfeldi* so nearly that a full description is unnecessary; I give only the distinguishing points:—

THALASSOMYIA AFRICANA, sp. n.—Antennæ slightly longer than in *T. frauenfeldi*, the intermediate flagellar segments rather more rounded. Male hypopygium showing slight differences; in particular the clasper is relatively smaller, its outer surface hardly concave, its tip more pointed, and the apical spine, which is distinct in *T. frauenfeldi*, is here hardly distinguishable from a hair. Front tibia longer, being fully one-fourth longer than the femur. Costa reaching well beyond the tip of the radius, but thinning out gradually. Media ending distinctly below the tip of the wing, so that the distance of its tip from the tip of the radius is rather greater than from the upper branch of the cubitus, whereas in *T. frauenfeldi* it is much less. Cubital fork rather shorter than in *T. frauenfeldi*, its lower branch more strongly curved downwards.

Length of body, about 2 mm.; wing, 2 mm.

TANGANYIKA: Dar-es-Salaam, 1 ♂ taken on or near seashore (*Dr. R. R. Scott*). Habits not noted.

## CAMPONTIA Johnston.

Described first as a worm, chiefly for the reason that in 1830 no marine insect larvæ were known, *Campontia eruciformis* has long been recognized as being a Chironomid larva, though its exact identity is still uncertain. Miall, quoted by Theobald (**28**), first suggested that it might be the same as *Thalassomyia frauenfeldi*, and there is little in Johnston's description and figure to disprove this suggestion, although both could apply about equally well to an *Orthocladius*. Johnston's larvæ were found between tide-marks among seaweeds in Berwick Bay, Northumberland, a locality from which no collections have been made since his time. It should be mentioned that Swainson, quoted by Theobald (**28**), has evidently confused two or more species, for the figure which he gives as representing the *Campontia* larva obviously refers to a *Chironomus* of the *dorsalis* group; it is this figure which has been copied by Johannsen (**12**) and discussed by Bezzi (**4**). Moreover, Johnston himself may have had more than one species, for he says in his description that "a few hairs terminate the anal segment," although his figure shows only two hairs, as in *Clunio*; the figure, however, is probably inaccurate, the posterior pseudopods shown being of the *Orthocladius* and not of the *Clunio* type. In view of the uncertainty the name *Campontia* cannot very well be adopted.

## HALIRYTUS Eaton and allied forms.

The genus *Halirytus* was established by Eaton in 1875 for some female specimens obtained between tide-marks in Kerguelen Is., Antarctic Ocean. Neither Eaton's original diagnosis nor Verrall's (**31**) rather fuller description mentioned the details of tarsal and tibial structure, which are to-day regarded as of great importance. Fortunately, however, Eaton's specimens are still in fair preservation in the British Museum, and from them it can be ascertained that the tibiæ are devoid of any trace of spurs or combs, and the last tarsal segment is trilobed at the tip, the median lobe finger-like and projecting over the long hairy empodium. A tarsus such as this is extremely unusual in the Chironomidæ, and is known only in a few other littoral forms. A further very peculiar feature which *Halirytus* shares with the littoral species just mentioned is the form of the ovipositor, the cerci being rather long and pointed and rather hard, almost like those of a Tipulid. In view of the close resemblance in these important features, it seems to me that all the forms listed below might well be placed in the single genus *Halirytus*.

No larvæ of this group are certainly known. Deby (**8**) does, indeed, briefly describe a larva which he attributes without question to *Psamathiomyia*, but, judging from his statement, this larva differs greatly from all known Chironomid larvæ and resembles a Tipulid. Thienemann (**29**) has therefore suggested, apparently with good reason, that Deby had described some quite different larva and not that of *Psamathiomyia*.

The species of this group at present known are the following:—

*Halirytus amphibius* Eaton.—Kerguelen I. Wings very much reduced in size, without distinct venation (at least in ♀; ♂ is unknown). Small halteres present. No scales on tibiæ. Palpi described as 2-segmented, but in a specimen I have mounted I only detect a minute nipple-like second segment on one palp, not on the other; this specimen also shows a reduction in the antennæ, which have only 4 segments instead of 5.

*Jacobsiella magellanica* (Jacobs).—Straits of Magellan. Wings much reduced in both sexes. Halteres stated to be absent, but this is possibly an error, and, if so, the species may be the same as *H. amphibius*. Palpi with a single segment. Male claspers not serrate The species was originally described as a *Belgica*, the genus *Jacobsiella* being erected subsequently by Rübsaamen (**26**).

*Psamathiomyia pectinata* Deby.—S. France. Wings much reduced in both sexes. Short halteres present. Palpi with two segments. Tibiæ without scales. Male claspers strongly serrate on the outer margin. The larvæ are stated to feed on *Enteromorpha*.

*Paraclunio trilobatus* Kieff.—California. Wing fully developed, with a venation like *Chironomus* (in ♀; ♂ is unknown). Femora and tibiæ with rows of lanceolate scales; tarsi with fasciculate

hairs. Larva stated to occur among rocks on shore in company with *Haliotis*, but no description has been published.

*Trissoclunio fuscipennis* (Kieff.) and *T. minor* (Kieff.).—Cape Town. Differ from *Paraclunio* (under which name the species were at first described) in having no scales on the femora and tibiæ and no fasciculate hairs on the tarsi. Nothing is known of the early stages or habits, except for Péringuey's remark (quoted by Kieffer) that the insects "flit along the shore on dark nights."

### Eretmoptera Kellogg.

As described by Kellogg (**16**) this has the fourth tarsal segment cylindrical, the fifth simple; empodium long; each tibia with a single spur; ovipositor short and inconspicuous; wings reduced and strap-like in both sexes; palpi long, 3–4 segmented; antennæ with 6 segments in the male, 4 in the female; eyes pubescent. The genus therefore appears quite distinct alike from *Clunio*, *Halirytus*, and *Thalassomyia*. The statement that the eyes are pubescent suggests that it may perhaps be a *Trichocladius* in which the wings have been reduced and the male antennæ have approximated in structure to those of the female. The presence or absence of the hind tibial comb is unfortunately not stated. The type, *E. browni* Kell., was found on the rocky coasts of California, the adults being in large numbers and skimming rapidly over the surface of the water.

A second species, *E. murphyi* Shaeffer, has been described from South Georgia. This, however, differs from *E. browni* in having bare eyes, and it is doubtful if it should be placed in the same genus; nor does it appear to be truly a marine form. It is probably identical with *Belgica antarctica* Jacobs, a subapterous form described from the same region. According to a note by Racovitza in the paper by Rübsaamen (**26**), this species breeds in small rock-pools, presumably of fresh water. containing moss. Kieffer, in an appendix to Thienemann's paper on Swedish Chironomidæ (**30**), states that *B. antarctica* has the typical hind tibial comb of the tribe Orthocladiariæ, and it is probably a degenerate *Orthocladius*.

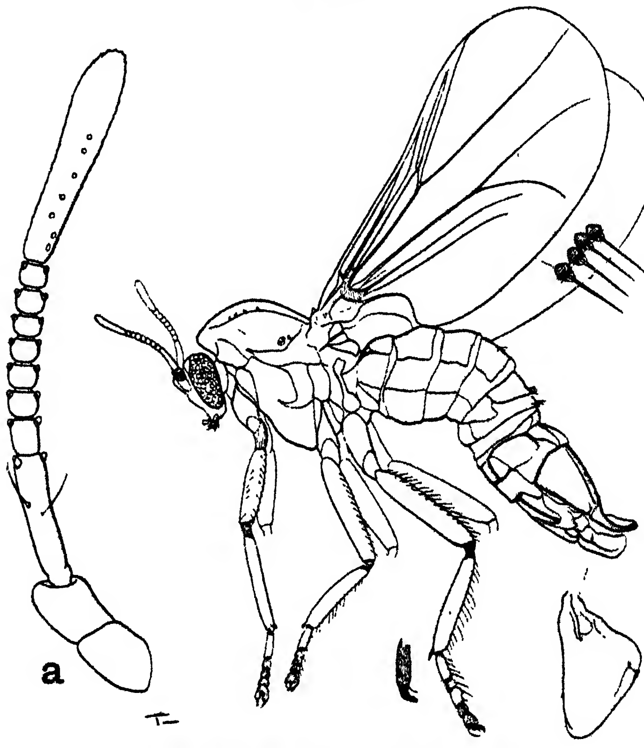
## B. Some New Species from Samoa.

Among the marine organisms collected by P. A. Buxton and G. H. E. Hopkins in Samoa were four species of Chironomidæ. One of these belongs to the genus *Clunio*, and is of interest as greatly extending the known range of this genus, which had hitherto been found only on European coasts: two others are species of *Tanytarsus*, the first members of this genus to have been found breeding in salt water, and the first representatives of the tribe Chironomariæ known to breed in the sea; the third exhibits such remarkable modifications of adult structure that a new genus has to be created for it. I will first describe the four new forms and then proceed to discuss the affinities of the new genus.

CLUNIO PACIFICUS, sp. n. (Text-fig. 2.)

This so much resembles the European *C. marinus* Hal. that it is only necessary to call attention to the differences, which are as follows:—Segments 4–10 of the antennæ are rather shorter, 9 and 10 in particular being slightly shorter than broad; 4–6 are distinctly pale at the base, especially on the under side, instead of all dark as they are in *C. marinus*; 11 is more slender, being hardly any stouter than the others, and relatively longer,

Text-figure 2.




*Clunio pacificus*, sp. n. ♂. *a*. Antenna.

being fully as long as 4–10 together. The abdomen (in spirit specimens) appears to have the basal segments greenish, only the last few being dark. Claspers slightly different in shape, without the recurved tip which is present in *C. marinus* and *C. balearicus*. Knees and articulations of the tarsal segments more conspicuously dark; on the front and middle legs the last four and on the hind legs the second and fourth tarsal segments almost entirely dark. (In *C. marinus* the tarsal articulations

are dark on the under side only.) Hind tarsi considerably shorter, all the segments relatively broad in proportion to their length, the second being as broad as long. Spur of the hind tibia rather shorter and conspicuously hooked, that of *C. marinus* being only slightly curved at the tip. Venation: Costa and radius shorter, the latter straight. *M* nearly straight, only very slightly curved upwards, so that the distance of its tip from the tip of the costa is much greater instead of much less than from the tip of *Cu* 1. Cubital fork narrow at the base, *Cu* 2 not being nearly so strongly recurved as in *C. marinus*. Length of body, about 2 mm.; wing, about 1·5 mm.

Apia, Upolu Island, "abundant in air over sea-shore, 8 P.M., 11. xii. 1925, Pilot Station" (*P. A. Buxton*). Cotypes, 3 ♂ preserved in spirit. Female and early stages not obtained.

TANYTARSUS HALOPHILÆ, sp. n. (Text-fig. 3, *c* and *g*; text-fig. 4, *a*, *b*, *d*, *g*, and *h*; text-fig. 8, *e*.)

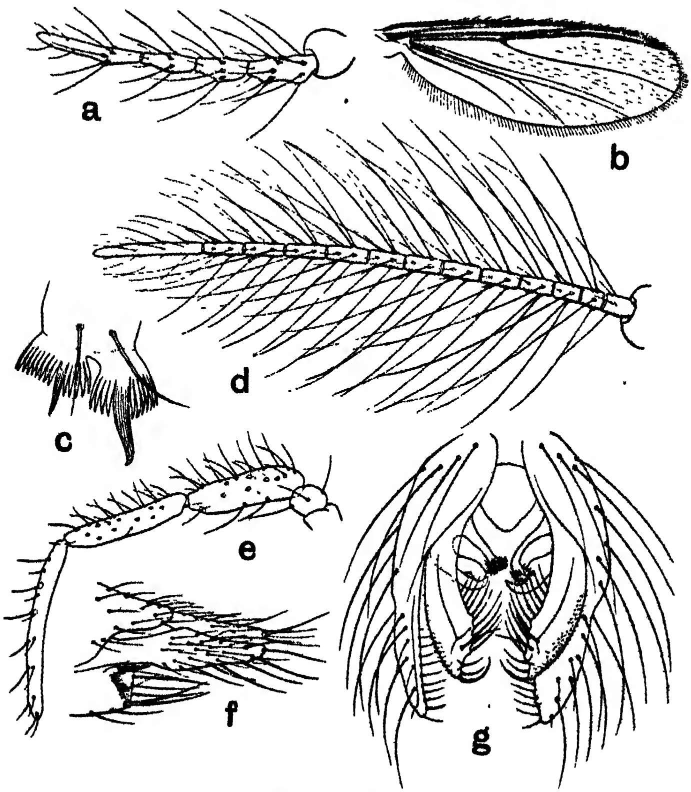
*Male.*—Eyes bare, reniform, widely separated, the distance between them being rather greater than their vertical length. Front practically smooth, without papillæ. Antennæ (compare text-fig. 3, *d*, antenna of *T. maritimus*) with 1+13 segments, all the flagellar segments except the last are about twice as long as broad and bear two long verticils; last segment only as long as the preceding three together, with about three short hairs at its tip. Palpi with four segments, first about as long as broad, second and third about three times as long, fourth half as long again as the third. Scutellum with two long bristly hairs placed rather close together, as well as some shorter ones. Hypopygium (text-fig. 3, *g*) of the normal structure for the genus; claspers not suddenly narrowed at the tip; side-pieces with three pairs of basal appendages, the ventral one with a rather slender stem and terminal knob covered with a dense brush of simple curved hairs. Front tibia without comb or spur. Combs of posterior tibiæ (text-fig. 3, *c*) distinctly separate, together occupying hardly more than half the circumference of the tibia; one with a long spur which is nearly twice as long as the comb itself, the other with a much shorter but distinct spur. First segment of front tarsi about 1·7 times as long as the tibia. Empodium and pulvilli small, about one-third as long as the claws. Wings moderately hairy all over; anal area fairly well developed; venation not ascertainable, but probably normal.

*Female.*—Antennæ with 1+4 segments; 2–4 about twice as long as broad, very slightly fusiform, without distinct necks, and with a median verticil of hairs which are about twice as long as the segments; 5 rather under twice as long as 4, with a sub-basal verticil of long hairs and about three short hairs at the tip. Cerci pointed and rather long. Other characters of the head, thorax, legs, and wings as in the male.

*Pupa.*—Differs from the majority of pupæ of this genus described by Bause in having no trace of a prothoracic horn.

(It is just possible that these organs have been broken off the two pupæ examined.) Thoracic integument apparently quite smooth. Dorsal ornamentation of abdomen consists of pairs of small round spots on each of segments 2–6; these spots are all of approximately the same size, and the small spines composing

Text-figure 3.

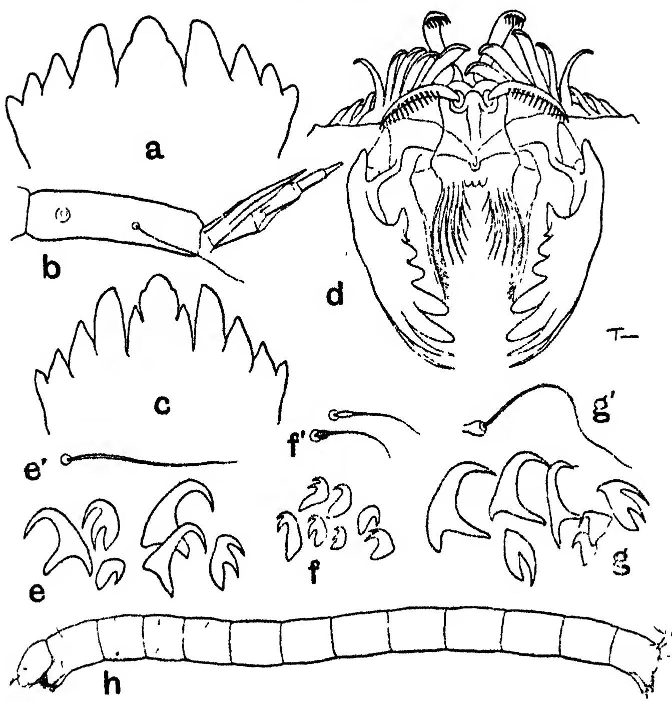



*a, b, d, e, f,* details of *Tanytarsus maritimus*, sp. n. *a.* Antenna of ♀. *b.* Wing of ♀. *d.* Antenna of ♂. *e.* Palpus. *f.* Genitalia of ♀.—*c* and *g*, *Tanytarsus halophilæ*, sp. n. *c.* Tip of hind tibia, showing combs and spurs. *g.* Hypopygium of ♂.

them are stronger and darker on the anterior portion of each. The transverse line of spines on the posterior margin of the second segment (text-fig. 8, *e*) runs straight across almost the entire width. The finer abdominal ornament (visible under a high power) consists of minute points of chitin scattered rather irregularly over about the posterior half of each segment except

the first; in the male at least these points are not more conspicuous on the terminal segment. The lateral margin of the eighth segment bears one fine hair (or two?) near the middle, and two more close together near the posterior end; at the posterior lateral corner of this segment is a group of about five or six stout thorns, not arranged in a very definite comb. Each

Text-figure 4.




Details of larval morphology of *Tanytarsus halophilæ*, sp. n.; *T. maritimus*, sp. n.; and *Pontomyia natans*, gen. et sp. n. *a*, mentum; *b*, antenna; and *d*, labrum, with its various appendages of *T. halophilæ*. *c*. Mentum of *T. maritimus*. *e*. Selected spines from posterior pseudopod, and *e'* lateral hair from an abdominal segment of *T. maritimus*. *f* and *f'*. The same structures in *P. natans*. *g* and *g'*. The same in *T. halophilæ*. *h*. *T. halophilæ*, whole larva, to show general form of body.

anal paddle has two dorsal hairs and a fringe of about 35 long hairs.

*Larva* (text-fig. 4, *h*).—Agrees well in the main with Bause's detailed generic diagnosis, but differs in a number of points from all the species described by him, particularly in the very slight development of the antennal base, which is hardly half as

long as broad, and the structure of the labium. The antennæ (text-fig. 4, *b*) are 5-segmented: first segment nearly four times as long as broad and slightly longer than the remaining four segments together, the hair placed somewhat beyond the middle; second segment with its Lauterborn's organs rather large and sessile (I cannot be certain whether there are two of these or only one), apparently no papilla; third segment more slender than the second but not much shorter; fourth, again, more slender but of the same length as the third; fifth small and conical. Frontal hairs simple, not branched or fringed. The five lateral appendages of the labrum (text-fig. 4, *d*) somewhat spathulate, their apical margin not fringed. The pre-mandibles are provided with five teeth, of which the two basal ones are small, the next two large, with rounded tips, and the apical one large but more slender and pointed. Mandibles with five teeth. Mentum (text-fig. 4, *a*) with a large middle tooth which carries a small denticle on each side but is not split or emarginate in the middle; outside this are only four teeth on each side, the first very large, almost equalling the median tooth, the others much smaller. If I have rightly identified the bristles representing the larval legs on each thoracic segment, these are only two in number, both long. The double-feathered bristles, laterally placed at the apex of segments 2–6 of the abdomen, which are said by Bause to occur on all *Tanytarsus* larvæ, are present in this species also, but are small and difficult to detect. Each of segments 3–7 bears latero-ventrally near the base a simple hair (text-fig. 4, *g'*). The dorsal tubercles on the last segment bear, in addition to the bunch of eight long hairs, two short ones, one shorter than the other. The hooks in the posterior pseudopods have the horseshoe-like arrangement described by Thienemann and Bause as characteristic of the genus; the individual hooks (text-fig. 4, *g*) are large and number only 16 in each pseudopod, the largest being simple, the others being formed of two or three spines united by a common base. The anal gills, if present, are very small; I have not been able to detect them.

Length of full-grown larva about 4 mm.; pupa and adult barely 2 mm.

Fagamalo, Savaii Island, xi. 1925; numerous larvæ, one male pupa and one female pupa skaken from *Halophila* plants (*P. A. Buxton* and *G. H. E. Hopkins*). The characters of the adults have been described from those contained in the two pupæ; all details could be made out except those of colour and venation.

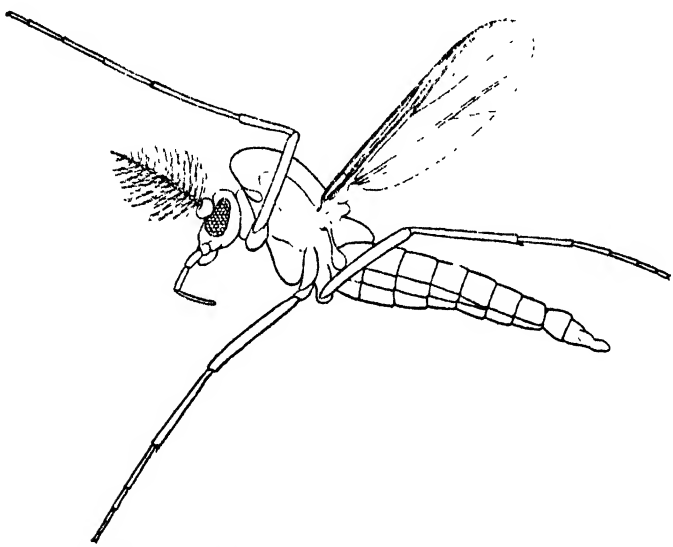
**Tanytarsus maritimus**, sp. n. (Text-fig. 5; text-fig. 3, *a–f*; text-fig. 4, *c*, *e*.)

*Male* (text-fig. 5).—Uniformly pale yellowish. Structural details of antennæ and legs as in *T. halophilæ*. Hypopygium also similar, but the ventral basal appendage longer, not clubbed at the tip, and covered with much longer hairs, which, though

denser towards the tip, occur on nearly the whole appendage, except at the base. The other basal appendages also rather differently shaped. Wings very scantily haired; apart from those on the veins, the only macrotrichia are a few round the tip and a row in cell *R* 5. Venation normal; *R* 4+5 somewhat curved and running close to the costa; *r–m* nearly horizontal; *fCu* well beyond *r–m*.

*Female.*—Colour as in the male. Antennæ (text-fig. 3, *a*) much as in *T. halophilæ*, but segments 3 and 4 rather more slender at each end. Macrotrichia of wings (text-fig. 3, *b*) much more numerous than in the male, being scattered fairly densely

Text-figure 5.



*Tanytarsus maritimus*, sp. n. ♂. (The hairs, except those at the tip of the wing, are omitted.)

over most of the wing (as in both sexes of *T. halophilæ*). Cerci (text-fig. 3, *f*) still longer and more pointed than those of *T. halophilæ*.

*Male pupa.*—Resembles that of *T. halophilæ* so closely that no differences could be discovered.

*Larva.*—Very closely resembles that of *T. halophilæ*, but the lateral denticles of the middle tooth of the labium are much more distinctly separated off from the main portion; the anterior pseudopods have a ring of fine but longish teeth at the base, while in *T. halophilæ* they decrease regularly in size towards the base of the pseudopod; the latero-ventral abdominal hairs

(text-fig. 4, *e'*) lack the basal papilla; and there is a slight difference in the shape of the teeth in the posterior pseudopod (text-fig. 4, *f*).

Apia, Upolu Island; adults of both sexes very numerous in company with *Clunio pacificus*, 8 P.M., 11. xii. 1925 (*P. A. Buxton*). Besides those taken on the wing, a number of females and one or two males were found in the tow-net. Cotypes, 2 ♂, 5 ♀ in alcohol. Empty male pupal skins and a few larvæ taken at the same place among *Halophila* plants, 22. ii. 1925, are presumed to belong to this species.

These two species of *Tanytarsus* do not fit precisely into any of the divisions which have been proposed recently by Kieffer as genera, but they appear to come nearest to his *Tanytarsus* in the restricted sense. Their most striking peculiarity is the very short terminal segment of the male antennæ, most if not all the other species having this segment as long as or longer than the preceding 12 together. The larvæ fall, according to Bause's arrangement, near the *lauterborni* group, although the pupæ show points of affinity with the *virens* group. In no stage are there any characters which would warrant the separation of these species from the genus *Tanytarsus*.

## PONTOMYIA, gen. n.

*Male.*—Antennæ 15-segmented, long, slender, and bare. Palpi large, 2-segmented. Labium atrophied. Tip of abdomen permanently rotated through 180°. Front legs long; first tarsal segment longer than the tibia; no claws. Mid legs remarkably short and rather stout; claws of peculiar structure. Hind legs long; claws rudimentary: no tibial comb or spurs; no empodium. Wings reduced in size and of peculiar form, the basal part puffed out, the tip flattened and jointed; venation not clearly distinguishable.

*Female.*—Vermiform, without appendages except for the rudimentary posterior legs.

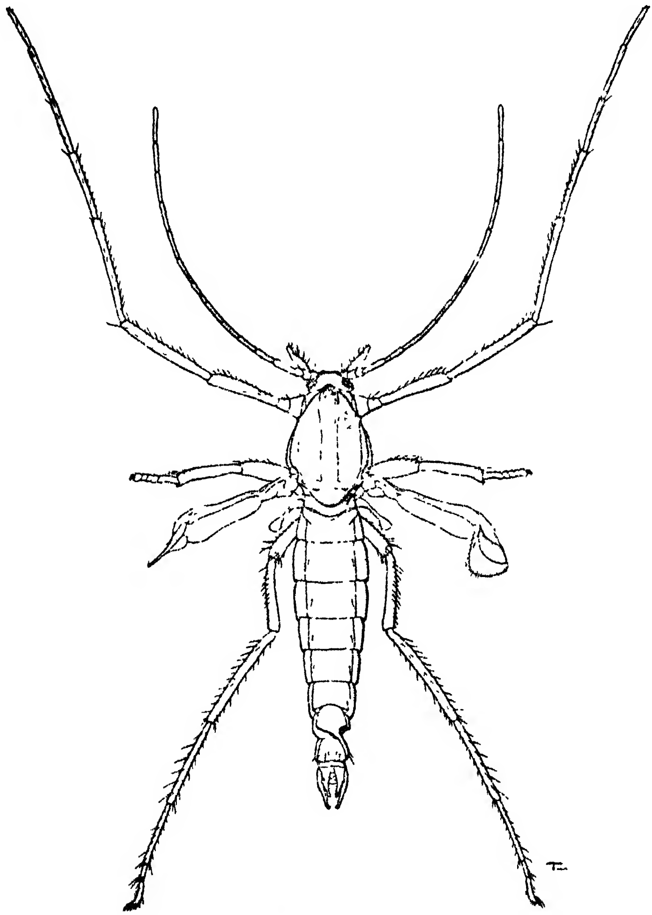
*Larva* and *Pupa* resembling those of *Tanytarsus*.

PONTOMYIA NATANS, sp. n. (Text-figs. 6 & 7; text-fig. 8, *a*-*d*; text-fig. 4, *f*.)

*Male* (text-fig. 6).—*Head* broad, closely applied to the thorax, quite smooth and bare. Eyes widely separated above, bare; seen in side view they are somewhat dumb-bell-shaped, the lower swollen portion being somewhat larger than the upper; in all there are only about 20–25 facets. Antennæ 15-segmented, the first three segments subequal in size and hardly longer than broad; remaining segments slender and cylindrical, devoid of bristles, and clothed only with fine short uniform pubescence, each at least 3·5 times as long as broad, the last few rather more slender and proportionately longer; segments 5–10 are somewhat darkened, the rest practically colourless. Palpi (text-fig. 7, *f*)

large, rigid, bristly, projecting forwards and more or less divergent, composed of only two distinct segments, the first about twice as long as broad, the second over three times as long as the first, suddenly narrowed and constricted a little before the tip. Labium very much reduced, hardly distinguishable. *Thorax* of the usual

Text-figure 6.

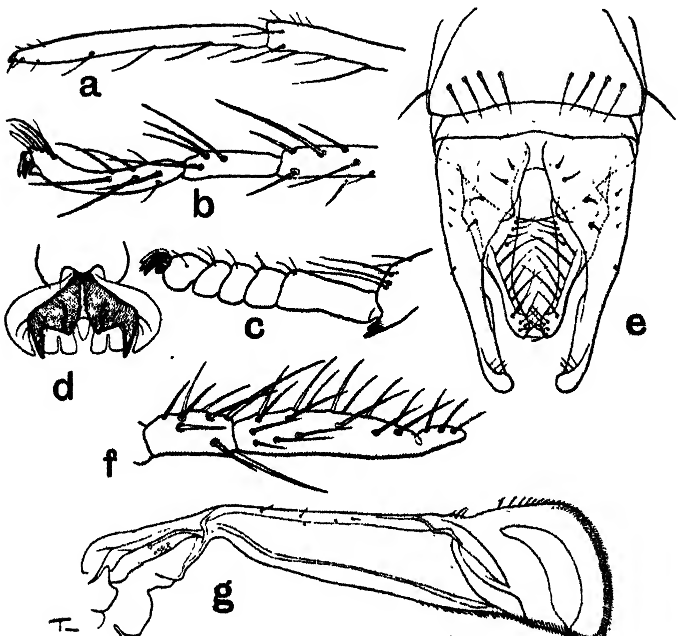


*Pontomyia natans*, gen. et sp. n. ♂.

Chironomid form, but quite bare except for some short pubescence on the scutellum; the usual three mesonotal stripes brownish, the ground-colour pale. Prothorax much reduced, completely divided dorsally. Spiracles present and also tracheæ; but whether

the spiracles were actually open could not be definitely ascertained. *Abdomen* somewhat tapering towards the tip; nearly bare, only one pair of fine bristles being present on each segment except the last, which has a row of them. The seventh segment in all the specimens has a somewhat asymmetrical form, owing to the permanent inversion (probably after emergence from the pupa) of the eighth and ninth segments. Spiracles apparently rudimentary and closed. Hypopygium (text-fig. 7, *e*) of rather simple

Text-figure 7.




Morphological details of *Pontomyia natans*, gen. et sp. n. ♂. *a*. Tip of front tarsus, showing absence of claws. *b*. Tip of hind tarsus. *c*. Tip of middle tarsus. *d*. Middle claws, further enlarged. *e*. Hypopygium. *f*. Palp. *g*. Wing.

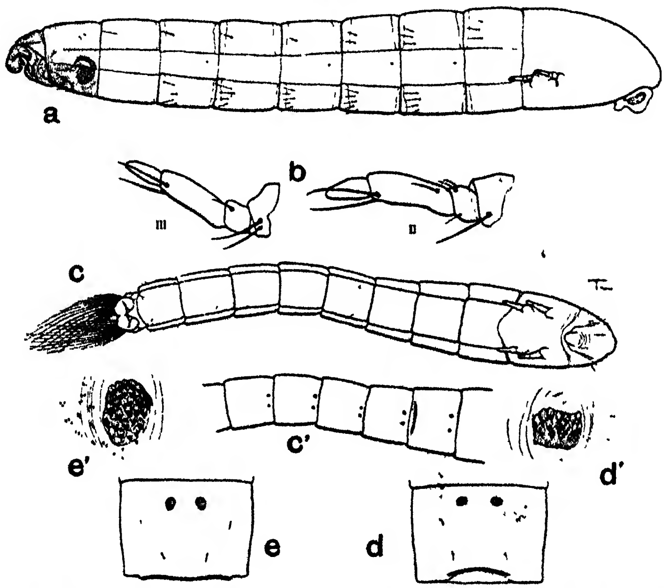
structure; the claspers rigid, extended straight backwards in a line with the side-pieces; only one pair of basal appendages, which are large and provided with numerous recurved bristles. *Front legs*: Coxæ large, very broad in proportion to their length, together with the trochanters forming a sort of cone. Femora rather short, simple at the tip. Tibiæ a little longer and more slender than the femora, without spur or scale. First tarsal segment very slightly longer than the tibia, second and following segments shorter; last segments (text-fig. 7, *a*) devoid of any

trace of claws, empodium, or pulvilli. The femur, tibia, and first two tarsal segments are slightly fringed on the inner side with bristly hair. *Middle legs*: Coxæ small. Femora short and noticeably thicker than the front pair; tibia also rather short and stout, the tip produced on the under side and blackened, but no true spurs present. Tarsus (text-fig. 7, *c*) remarkably short, all the segments together only about two-thirds as long as the tibia; first segment about three times as long as broad, the others rather broader than long. Claws (text-fig. 7, *d*) large, of peculiar form, with large basal prominence; below the claws is a membranous structure divided into seven lobes as shown in the figure, presumably representing the empodium and pulvilli; it is extremely difficult to see owing to its thinness and transparency. *Hind legs*: Coxæ small. Femora and tibiæ rather short and stout; the femora, however, not so distinctly thickened as those of the middle legs. Tibiæ rather bristly on the outer side, without any trace of apical spurs or combs. Tarsi very long and bristly, the first segment fully half as long again as the tibia; fourth segment cylindrical, but much shorter than the fifth, which is of peculiar shape (text-fig. 7, *b*), concave above and convex below. Claws rather small; no empodium or pulvilli, but a small ventral tubercle is present below and before the claws. *Wings* (text-fig. 7, *g*) of remarkable shape, the basal two-thirds in nearly all the specimens being approximately cylindrical through the puffing-out of the internal space, while the tip is flattened and more strongly chitinized. Moreover, the whole wing is twisted close to the base, so that when it is fully extended the costal margin occupies a dorsal instead of an anterior position as in the normal insect wing. Again, the puffed-out portion is practically bare, while the flattened tip is finely fringed all round; the hairs in this fringe are mostly inserted well inside the margin instead of round the edge as usual. Between the swollen and the flattened portions of the wing there is a false joint, extending obliquely across the wing; by manipulating the extended wing with needles it is easy to ascertain that slight pressure from the front will fold back the flattened tip, while similar pressure from behind will not bend it forwards. Inside the flattened tip is a crescent-shaped thickened patch, while at the joint are two or three thickened areas; these thickenings do not appear to have any clear connection with venation. Of the true veins, only the costa can be made out clearly, and that only on the swollen portion; the cubitus also seems to be indicated as a simple vein. Halteres normal.

*Female* (text-fig. 8, *a*).—*Head* small, closely applied to the thorax. Eyes small and oval, with only about 8–10 facets. No trace whatever either of mouth-parts or antennæ. *Thorax* without any sign of segmentation. No trace whatever of wings, halteres, or front legs; the four posterior legs (text-fig. 8, *b*, II. and III.) being represented by tiny rudiments, with two short basal segments presumably representing the coxa and trochanter, a longer one with two apical ventral hairs which may be taken as

the femur, and a small terminal one. Prothoracic spiracle present, but apparently overgrown by skin; metathoracic spiracle not detected. The thoracic integument is bare and very feebly chitinized. *Abdomen* cylindrical, feebly chitinized except for the terminal segment, which is much stronger, so that in stained specimens it appears to the naked eye as the head. Six pairs of small non-functional spiracles. Tergites 1 and 2 each with three lateral hairs, tergite 3 with two, and tergites 4–7 each with one;

Text-figure 8.




*a. Pontomyia natans*, gen. et sp. n. ♀ adult. *b.* The same, leg-rudiments (II. and III.) further enlarged. *c. P. natans*, ♀ pupa, ventral view. *c'.* Segments 2–6 of pupal abdomen, dorsal view showing ornamentation of the *Tanytarsus* type. *d. P. natans*, second abdominal segment of ♀ pupa. *d'.* Anterior spot further enlarged to show constituent spinules. *e* and *e'.* The same in ♂ pupa of *Tanytarsus halophilæ*, sp. n.

sternites 2–6 each with a transverse row. Cerci rounded and downwardly projecting.

*Female pupa* (text-fig. 8, *c*).—The appendages of the head and thorax are no better developed than those of the adult, there being no trace of the antennæ, mouth-parts, or front legs. In the specifically pupal characters there is a great resemblance to *Tanytarsus halophilæ.* The prothoracic horn (respiratory trumpet) is absent, its place being occupied by a hair. The paired spots of spinules on abdominal segments 2–6 (text-fig. 8, *c'*) and the row of microscopic teeth across segment 2 (text-fig. 8, *d*) are almost

exactly the same as in *T. halophilæ*, but the row of spinules is shorter, and there is a difference in the minor ornament of the abdomen, which here consists of numerous microscopic points of chitin arranged in lines which form an irregular network on the anterior part of each segment except the first; they are more strongly marked on the last segment. There are no lateral hairs on any of the abdominal segments and no spines at the apical corners of the penultimate segment; the paddle-fringe includes about 25 instead of about 35 hairs, but has two dorsal hairs as in *T. halophilæ*.

*Male pupa.*—Not obtained, unless the skins referred to under *T. maritimus* really belong to *P. natans*; if so they differ from the female in possessing the usual spines on the penultimate segment. Such a form of sexual dimorphism in the pupæ would be very unusual but not impossible.

*Larva.*—If correctly associated with the adults, shows the following characters:—Generally extremely similar to that of *T. halophilæ*, the structure of the head (antennæ, labrum, mentum, etc.) being practically identical; abdominal structures also very similar. The only striking difference is in the hooks on the posterior pseudopods (text-fig. 4, *f*), which are much smaller, rather differently shaped, and much more numerous (60–65 in number instead of only 16). In addition, the latero-basal hair on each of abdominal segments 3–7 instead of being simple has a peculiar swollen base (text-fig. 4, *f′*). The minute spines on the anterior pseudopods are rather differently shaped, but there is no basal ring of slightly longer ones such as occurs in *T. maritimus*.

Length of male body, 2 mm. (excluding antennæ); antennæ, 1·6 mm.; wing, 0·8 mm.; female about 2·5–3 mm.; full-grown larva about 5 mm.

Apia, Upolu Island. Large numbers of males and a few females obtained under circumstances described by P. A. Buxton in the paper following this, among *Halophila* plants.

## Discussion.

The material at first sent home by Dr. Buxton comprised a large number of males, four or five females, and a single cast pupal skin of a female of *Pontomyia natans*. The pupal skin was obviously one from which a vermiform female had hatched; and since all were taken together, the assumption appeared justified that males and females belonged to one species. Owing to the extreme reduction of the female and the extreme specialization of the male, an attempt to ascertain the probable affinities of the species was rendered very difficult. Certain indications, however, appeared to point to some connection, apparently rather remote, with *Chironomus* or *Tanytarsus*: these were the rather long first segment of the front tarsi and the rigid, backwardly-extended claspers of the male; also the abdominal ornamentation and the fringed paddles of the pupa. The pupal features appeared to be

decisive, since the resemblance to some European species of *Tanytarsus* described by Bause was most striking, and this type of ornamentation is quite unknown in any other genus of the family.

This conclusion as to the origin of *Pontomyia* was confirmed in a remarkable way when additional larval and pupal material brought home by Dr. Buxton in January 1926 was examined. This material was obtained off Savaii Island under conditions almost identical with those under which *Pontomyia natans* was found at Apia; it included two mature pupæ which on dissection were found to contain a male and female of a quite normal *Tanytarsus*, *T. halophilæ*. As described above, the pupæ, and probably also the larvæ, of *P. natans* and *T. halophilæ* are extremely similar. Now we know from the researches of Thienemann and others that the genera and often the species of Chironomidæ show very well-marked distinctions in larvæ and pupæ, these being often more marked than the differences in the adults. We seem to be justified, therefore, in concluding that we have in *T. halophilæ* a representative of the stock which has produced *P. natans*.

Another representative of this same stock is seen in *T. maritimus*, the existence of which was not suspected until after the discovery of *T. halophilæ*, when it was found that two species were represented among the larvæ collected with *P. natans* in Upolu, and that *Tanytarsus* adults had been collected on the wing in the same locality; it seems only reasonable to assume that the larva which more nearly resembles that of *T. halophilæ* is the larva of the second *Tanytarsus*, and that the other larva is that of *P. natans*.

As all these larvæ live under identical conditions and belong to the same stock, it is natural that they should resemble one another closely. What is very surprising is that the adults of one of the three species should have become modified in such an extraordinary manner. It would seem at first sight that the changes have been sudden and complete, as it is difficult to imagine intermediate stages between midges that mate and oviposit in the air in the normal way (*Tanytarsus*) and one that remains throughout life under water (*Pontomyia*). That such intermediate stages must have existed is almost certain, and it is hoped that some of them may yet be found in some part of the Pacific. A possible explanation of the reason for this remarkable departure is that in *Tanytarsus* (at least in that section of the genus to which *T. maritimus* and *T. halophilæ* belong) the empodium and pulvilli are rudimentary. Without these organs an insect which took to mating on the ground instead of in the air might find it difficult or impossible to move freely over wet rocks or the surface film of rock-pools, and might therefore be compelled to enter the water.

Most if not all the peculiarities of the male *Pontomyia natans* may be explained as consequences of or adaptations to a life

under water. The ordinary plumose and almost rigid antennæ of a male midge would obviously be a serious inconvenience to a swimming organism, but with the loss of the plumes and the lengthening of the segments the resulting whiplash-like appendage could easily be trailed behind during progression through the water. The outward curvature of the antennæ (see text-fig. 6) which is shown in most of the preserved specimens is very unusual in the Nematocera, and suggests that they may be folded back along each side of the body. The loss of the antennal plumes is not unnaturally accompanied by a reduction in size of the second segment of the scape, which in the dancing midges is enlarged to contain the "chordotonal organ." Probably the enlarged bristly palpi are to be regarded as a compensatory development for the loss of sensory function in the antennæ.

The rather unusual form of the front coxæ and trochanters would doubtless allow the whole front leg from the base of the femur to be turned backwards. The entire loss of claws on the front legs clearly shows that these are not used for walking, and the same is almost certainly true of the hind legs, for, owing to the reduction of the claws and the shape of the last tarsal segment, it is difficult to see how the insect could obtain a foothold. It is not surprising, therefore, to learn from Dr. Buxton's account that the long front and hind legs are used in swimming, although they do not appear to be specially adapted to this purpose. The slight fringe on the front legs may possibly be of some assistance, but it is not in any way comparable to the strong fringe which is developed on the legs of many aquatic beetles and Hemiptera. On the other hand, the wings are so remarkably modified that it is difficult to resist the conclusion that they are the main swimming organs, in spite of Dr. Buxton's statement (see the following paper) that he never saw them in use as such. The twisting of the wing to occupy a vertical instead of a horizontal position; the puffing-out of the basal part, thereby reducing its surface*; the hardening of the flattened tip and the form of its fringe; and, finally, the flexibility of this tip in a backward direction only can hardly be explained except by supposing that the wings are used as paddles. In many of the marine Chironomids discussed in the first part of this paper the wings are reduced, but no such modifications are found.

The short thick middle legs are apparently suited for grasping, and may either be used for maintaining a hold on the food-plant while the current is strong, or for holding the female during pairing. I am unable to suggest the use or reason of the peculiarly-formed claws of the middle tarsi. The twisting of the hypopygium is almost unique in the family Chironomidæ, though universal in the Culicidæ and Psychodidæ, and occurring sporadically in a few genera of the Tipulidæ. The significance of this

* In a few specimens the wing is not thus puffed out, the basal part being apparently rolled up instead, so that the paddle-like appearance of the whole wing is even more pronounced. It is possible that this is the normal condition af the wing in life.

structure has been discussed recently in a paper by Dr. C. G. Lamb. It is connected with the attitude or pose adopted preliminary to pairing, and implies a method different from that used by other members of the family. That such should be the case is not surprising in view of the worm-like character of the female, who could be capable at most of a feeble wriggling motion. The fact that the terminal segment of the abdomen is the only part of the female's body which is distinctly chitinized suggests that she remains in the pupal mud-tube with only her tail extended. Probably the male grasps this tube, and assuming that the female faces away from the male; the torsion of the hypopygium would, as explained by Lamb, be necessary for the "direct correlation" of the dorsal and ventral aspects of the genital tubes of the two sexes. It appeares significant that this permanent torsion also occurs in *Clunio*, another genus with a wingless female.

Another peculiarity of the male is the absence of the tibial spurs and combs. What the reason for this may be is not easy to see, but it is noteworthy that all other marine genera of Chironomidæ have also lost the hind tibial comb. A further sign of degeneration is to be seen in the simplification of the hypopygium, which, instead of the three pairs of basal appendages characteristic of *Tanytarsus* and well shown in *T. maritimus*, has retained only one.

The female has carried reduction to a greater extreme than almost any other Dipteron, the one fly which has gone even further being *Ascodipteron*, which is parasitic in the skin of bats. Parasitism is indeed frequently associated with degeneration, as for instance in *Stylops* and other insects of various orders; but it cannot have anything to do with the present instance, which is more comparable to that of the case-bearing Psychid moths, the females of some of which have lost all trace of all their appendages. It is probable that, with the conditions under which *Pontomyia* lives, a gravid female who attempted active locomotion would be unable to maintain her position and would be washed away by the current; she must therefore remain stationary and wait for the male to find her.

In common with other sea-breeding Chironomidæ, all these Samoan species have lost the larval anal blood-gills and the pupal prothoracic respiratory horns. Why salt water should have this effect is unknown; the blood-gills are always well developed in freshwater larvæ of this family. A reduction in the size of the gills has been noticed by Lenz (23) in species of *Chironomus* breeding in salt or brackish water, and a similar reduction occurs in the larvæ of the salt-marsh mosquitoes.

Finally, it may be remarked that this genus appears to provide one more convincing proof of the great importance for taxonomic purposes of larval and pupal characters, the use of which in classification is so much decried by some systematists. From consideration of the adults only of *Pontomyia*, one could only

hazard an uncertain guess as to their affinities, whereas a study of the early stages appears to place the matter beyond any doubt. It is clear that a fundamental change in the habits of the adults has been accompanied by equally fundamental changes in structure, so as to leave little trace of their origin, and that the larvæ and pupæ in retaining their ancestral habits have also retained the ancestral morphology.

## Summary.

A general review is given of our present knowledge concerning marine midges in various parts of the world. These belong to several genera, and appear to have been derived from different branches of one tribe (Orthocladiariæ) of the family Chironomidæ. Some of the flies remain unmodified and may be found flying over rocks and seaweed; others have vestigial wings in one or both sexes, and these are found only at extreme low tides running on exposed rocks or over the surface of pools; none are truly submarine. The larvæ of these various species occur in all tidal zones, sometimes even those below the limit of exposure by the lowest tides. Among these species two new ones are described from British coasts and one from East Africa.

Four new marine species are described from Samoa. One of these is known only from adult males captured on the wing, and belongs to the genus *Clunio*, hitherto believed to be solely European. The other three, of which both larvæ and adults were obtained, belong to a different tribe (Chironomariæ), and were taken among *Halophila*, a higher plant which grows in sea water on the reef. Two of these are normal air-living flies, and are referred to the genus *Tanytarsus*. The third is submarine in all stages, and shows remarkable structural adaptations to this life. The male has greatly reduced wings and bare antennæ; it swims actively with its long legs. The female is without antennæ, mouth-parts, wings, halteres, or functional legs, the front legs not even existing as vestiges. This submarine insect is described as a new genus and species, *Pontomyia natans*, and reasons are given for believing that it has been derived directly from one of the species of *Tanytarsus* with which it is associated.

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# 39. The Colonization of the Sea by Insects: with an Account of the Habits of *Pontomyia*, the only known Submarine Insect. By P. A. Buxton, F.Z.S., London School of Hygiene and Tropical Medicine.

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The following observations were made in Samoa, most of them in the neighbourhood of Apia, island of Upolu. In that part of Samoa the shore is protected by a fringing coral-reef which lies about half a mile from the land: between it and the shore is the lagoon, in most parts only a few feet deep at low tide. The floor of the lagoon consists in some places of growing coral, in others of fragments of corals and other organisms, pounded up to a fine white sand. In certain places a proportion of fine mud is mixed with the sand, and where this is so one finds the plant *Halophila ovalis* J. D. Hooker. Prof. W. A. Setchell, of the University of California, tells me that the name *ovalis* is to be taken to indicate a group of short-leaved forms the inter-relationships of which are at present not well understood. The plant, which is a member of the Order Hydrocharitaceæ, resembles the familiar oar-leaved *Potamogeton* of Europe in its general appearance. It is in no sense an estuarine plant, but lives in pure salt water, frequently miles from the mouth of a stream: in the places in which it grows it is not exposed to the air except at dead low water. Members of this group of the genus *Halophila* have a wide distribution in coral-reef lagoons in the Pacific and Indian Oceans, including those of isolated oceanic islands: it is believed that they spread by means of floating fragments. Other members of the genus are found in all tropical seas, and some of the other species are estuarine.

If one draws a fine tow-net through the lagoon at night, in places where the *Halophila* grows, one sometimes catches large numbers of the small Chironomid midge, described above (p. 796) by Edwards as *Pontomyia natans*. I have frequently used the tow-net by day in places in which this insect was known to be occasionally common, and have never obtained a single specimen. I presume that they hide by day in the patches of *Halophila*, but I have never been able to find them, though I have frequently searched handfuls of the weed. It is an interesting fact that the ordinary marine plankton, consisting of Copepods, Chætognaths, small Polychæts, and the larvæ of fish, Crustacea, "worms," and many other organisms, can be obtained only at night. But even at night one cannot be certain of finding adult *Pontomyia natans* in spots near Apia in which they are sometimes abundant. I have records of tow-netting on six occasions, at or about the

time of high tide, between 8 P.M. and 10 P.M.: on five of these occasions I caught no midges at all; on the sixth I obtained one dead specimen. On the other hand I have used the tow-net after sunset, at half tide or low tide on five occasions, and caught *P. natans* each time. Once I caught several hundred males and a number of females in ten minutes in a ten-inch net.

At first it appeared that the absence of these midges from the tow-net at high tide could be explained in a simple mechanical manner. It might be supposed that the midges cling to the *Halophila* plant, and never willingly leave it, but that when the tide is rising or falling the current along the shore is strong enough to wash them away. This explanation is untenable; the male *Pontomyia natans* is not sedentary, but is an active swimmer; also I have twice failed to catch specimens when the tide was nearly high, and the current along the shore was so strong that I could hardly stand in three feet of water.

It is quite possible that the periodicity of the insect depends upon the lunar cycle, but I have not enough observations to prove that this is so: I was never able to obtain specimens when the moon was full or nearly full, even when the state of the tide appeared suitable. In some way at present not understood, the lunar cycle determines the life-history of certain marine animals (Fox).

Of the habits of the adult *Pontomyia natans* we know little. I have only once caught males and females in numbers, and that was on the occasion of the insect's original discovery, and the whole catch was killed before I examined it. But I have been able to observe a few live males on several occasions, by turning the contents of the net into a beaker and examining them with a lamp. The male swims actively through the water, using its long first and third legs (see text-figure 6 Edwards, *supra*). It is interesting and remarkable that it is able to continue to live and swim about in the strong tidal currents which scour the floor of the lagoon. I think that swimming is the normal mode of progression, but I have also seen males supported on the surface of the water, with head, body, and wings in the air, and legs beneath the surface, paddling through the water. I am not convinced that this is a normal activity. It may be that when the contents of the tow-net are emptied into the beaker, some of the insects become caught on the surface and are unable to submerge. I have never seen the wings used in locomotion, either on or beneath the surface, and I have never seen the insect skate on the surface with its legs.

Very early in the investigation I assumed that *Halophila* was probably the food and shelter plant of *Pontomyia natans*: my reasons were that I never caught the midges except in places in which the plant was abundant, and that as both plant and insect must, at some time in the past, have entered the sea from fresh water, it seemed reasonable to associate them with one another. I was also able to find Chironomid pupæ among the

leaves of *Halophila*, and I once caught a pupa in the tow-net, but I think that it had probably been dislodged from the plants over which I was wading at the time. I have also taken adult midges and empty pupa-skins in the net at the same time after dark. The female pupæ found on the *Halophila* and the empty skins are identical, and they show the same extreme reduction in the appendages as the adult insects (text-fig. 8, Edwards); this proves them the pupæ of *Pontomyia natans*.

Numbers of Chironomid larvæ can be found among the *Halophila* plants, by shaking a handful of leaves and stems in a basin. The larvæ are dark brown when mature, and to the naked eye they do not appear to contain hæmoglobin. They swim actively with a wriggling motion when they are disturbed from the plant. I have taken them in the tow-net, so I suppose that occasionally they leave the plant or are washed out of it by currents. The larvæ live in a very fragile tube of mud, which they construct between two leaves of *Halophila*. The leaves which they choose are generally old, and are covered with a growth of sedentary diatoms, minute Hydrozoa, Polyzoa, etc. I have dissected larvæ of *Tanytarsus* or *Pontomyia* from Upolu and Savaii, and found in the gut much mineral debris, and a small number of diatoms, on which I conclude that they feed: I have not been able to find any fragments which I could attribute to the *Halophila*, but all the gut-contents are so finely divided that I am not able to state that the larva never eats that plant. One frequently finds plants of *Halophila* of which the leaves have been gnawed, and this may well be the work of one or other of these Chironomid larvæ. If the food of these larvæ is diatoms it helps to account for the enormous geographical range of these marine Chironomid genera; had the food been the tropical *Halophila* it would have been more difficult to explain this distribution. Edwards (p. 802) finds difficulty in distinguishing the larvæ that belong to the three different Chironomidæ which I collected. In nature I did not notice any differences in habit between the larvæ, and did not appreciate that I had to deal with several different organisms.

These Chironomid larvæ are living associated with a purely marine fauna, among the *Halophila* leaves or in the muddy sand in which the plant grows. With them one finds many species of Polychæts, Gephyrea, Turbellaria, Actinians, small Hydrozoa, Gastropod and other Mollusca, many Crustacea (Amphipods, Tanaids, Crabs, etc.), and other forms of marine life.

The eggs of these insects remain unknown; one is inclined to assume that the vermiform female *Pontomyia natans* never leaves the mud tube in which the pupa is found, but this assumption is hardly justifiable, because the wingless female of *Clunio marinus* is carried about, paired to the male (Carpenter): the fact that females of *Pontomyia* have been taken in the tow-net, may be explained as a result of disturbance caused by the net.

Of the life-history of the species described above by Edwards as *Tanytarsus maritimus* very little is known. I took adults at Apia, Upolu Island, at 8 P.M., on 11 Dec. 1925, together with males of *Clunio pacificus* Edwards, and a few specimens of a species of *Culicoides* at present undescribed. The *T. maritimus* were very numerous and troublesome, crawling all over my defenceless face as I waded about the lagoon with a tow-net in one hand and a lamp in the other. The pupæ of the second species of *Tanytarsus* (*T. halophilæ*) were obtained at Fagamalo, Savaii Island, by shaking plants of *Halophila* in a basin; at the time I did not realize that they were not pupæ of *Pontomyia natans*. The *Halophila* at this place in Savaii, grows under conditions similar to those which I have described from Upolu.

I believe that *Pontomyia natans* is the only known insect which is submarine in all stages, and this raises a very interesting question. Nearly half a million species of insects have already been described, and they show extraordinary powers of existing in the most varied environments. I am not thinking now of their ability to inhabit the air and the soil, and to devour almost all parts of all plants, and almost all kinds of decaying matter, but I am thinking especially of those insects which live in water. These show a remarkable diversity of habits. Some are sedentary and tubicolous; others crawl on the bottom, swim actively in mid-water or skim the surface; some live in still water, others in rivers, rapids, and waterfalls. The great majority live in fresh water, but some forms have descended the rivers and are established in estuaries, of which the saline content is variable. Some eat diatoms and unicellular algæ, others extract nourishment from mud, many are predatory, others again eat various forms of decaying matter. Many insects live in fresh water in their early stages and in the air when they are adult. Some of the early stages require atmospheric oxygen from time to time, others respire through the cuticle, or specialized parts of the cuticle.

With all the varied wealth of insect life on land and in fresh water, it is surely remarkable that so very few insects have become adapted to a marine existence, even for a part of their existence. An insect passing from fresh water into the sea would meet obstacles differing from those which would confront one passing from the land to the sea: but in general terms one may say that there would be many obstacles, some physical, others chemical, others biological, and that the insect would require to surmount a combination of barriers if it passed from a lacustrine to a marine existence.

The most obvious physical barriers are the currents, the tides, and the waves. No one of these, alone, is insurmountable.

In the sea itself a large number of Collembola, Coleoptera, and Diptera (Miall, chap. xii., Wesenberg-Lund, pp. 460–462, Flattely and Walton, pp. 308–311), and Arachnids of six different families

(Abraham) live in the zone between high and low tide-mark. Here they encounter more powerful waves and currents than they would if they had been able to live below the level of low tide. Most of them escape from these adverse conditions by burrowing into the sand or mud, or hiding under seaweed, for the short period of their immersion. It seems that the Arthropods of this zone are really terrestrial forms; they are strictly limited by an inability to exist permanently under water; they respire atmospheric air, and they carry a supply of it which is sufficient for a limited period, but they are not truly aquatic, in that they do not respire through the cuticle. For this reason they have been unable to penetrate further into the sea.

Among the insects which live, at least in their early stages, in fresh water, there are many forms which are able to maintain their positions in rivers and even in mountain torrents, where they meet currents more violent than they would ever encounter in the sea. And there are other forms which live in the shallow margins of large lakes, where they must meet waves at least as great as those which they would meet in a sheltered inland sea. We think, therefore, that it is not the physical barriers alone which have prevented the insects from permanently colonizing the sea.

But there exists also a group of chemical barriers, for instance the salinity, and the presence in sea water of a variety of inorganic salts; it may be that magnesium salts, or sulphates or other substances, are incompatible with the life of certain types of aquatic insects. It appears that these obstacles are probably more important than any others. For instance, Thienemann and Schmidt, quoted by Wesenberg-Lund, have shown that in salt lakes in Westphalia a large and varied insect fauna can be found provided the salinity does not exceed 2·5 per cent.; in lakes of this class they found many species known also from fresh water, and they found representatives of Diptera, Rhynchota, Odonata, Trichoptera and Neuroptera: but if the salinity exceeded 2·5 per cent. they found but a few forms, all of which were Diptera. This is true in other parts of the world also.

The only insects which can live in water containing 3 per cent. or more of salts (*i. e.* water at least as salt as the sea) are Diptera: (to this there is only one exception, the Trichopteron, *Philaniscus plebejus* Walker, the habits of which are described by Hudson: it is found in both islands of New Zealand, the larva living in rock-pools near low water mark). It is perhaps remarkable that this power should be possessed by a highly specialized Order, and not by any of the more simple Orders of insects; the explanation is, perhaps, that the larvæ of the Diptera are more specialized for life under fresh water than those of other insects. Among the Diptera it is only members of the families Culicidæ, Ephydridæ, and Chironomidæ which can

inhabit salt waters. Larvæ of certain Culicidæ (Balfour) and many Ephydridæ can inhabit extremely salt inland waters, even those from which some of the saline constituents are actually crystallizing, but they cannot apparently live in the sea. The reason is, perhaps, that the larvæ of these two families respire atmospheric air, and obtain it by visiting the surface, and that the winds and waves prevent their living in the sea.

It is only the Chironomidæ which have been able to do this, and it appears that they have done so on several occasions, for the genera which occur in the sea are not closely related to one another, and they are found in nearly all the seas of the world. One surmises that several factors have contributed to the success of the Chironomidæ in this respect. All Chironomid larvæ have reduced tracheation and respire through the cuticle; they are, therefore, not under the necessity of coming to the surface of the sea where they would be exposed to winds and waves, and tides; they can live continuously below the level of those unfavourable influences. The pupæ of *Pontomyia* and of the two marine species of *Tanytarsus* described below from Samoa, show a corresponding adaptation; they have lost the prothoracic horns (respiratory trumpets), and presumably live an entirely subaqueous life, under water among the *Halophila*. The vermiform female of *Pontomyia* has closed spiracles, and perhaps never leaves the mud tube among the leaves of the plant.

Apart from these structural adaptations, which have assisted the larva, pupa, and even the imago, to live in the sea, there is a biological factor which has worked in the same direction. The larvæ of many Chironomidæ in fresh water eat diatoms, which are universally distributed in the sea; this has rendered it easy for insects of this family to enter the sea, and when they had done so to acquire an enormous geographical range. (The genera *Clunio* and *Thalassomyia* plus *Galapagomyia* are found both in the Atlantic and the Pacific.)

But even if the fact is established that no insects except the Diptera can live in water as salt as the sea one fails to understand why more Diptera have not done so, and why insects of other Orders have not gradually adapted themselves to increased salinity, as they have adapted themselves to altered conditions in so many other respects. In many parts of the world the transition from fresh to salt water is extremely gradual, for instance in the Baltic and the Caspian Seas. The Baltic as a whole is less salt than the oceans, and in the northern end the conditions are almost estuarine, and a considerable number of freshwater insects, especially larvæ, are found. The Caspian is still less salt, and along the south coast there are great shallow lagoons, fresh on the landward side, where the rivers from the Elburz run into them, increasingly salt where they discharge into the Caspian. Tidal changes are not great either in the Baltic or the Caspian, and it seems curious that insects have failed to adapt themselves to the conditions which prevail here.

One must remember that even if an insect overcame the physical and chemical barriers in passing from fresh water to the sea, it would still be confronted by the biological barriers. It might meet predators against which it had no adequate defence, and it would be forced to change its food. If our insect were itself predaceous, for instance an adult or larval Dytiscid Beetle, or a larval Odonatan, or Plecopteran, one can quite imagine it passing from river to estuary and thence to a shallow sea, adapting itself on the way from a diet of Oligochæte worms and insect larvæ, to a diet of Polychæte worms, and Amphipods or other small Crustacea: and in view of the protean adaptability of insects in fresh water we can easily imagine the predator going further than this and becoming pelagic.

So far as we know no predatory insects have ever succeeded in doing this. The only apparent exception are the Halobatidæ, a family of Rhynchota, related to the familiar Water Skaters (Hydrometridæ). The Halobatidæ skate on the surface of the ocean in the warm parts of the globe; in one sense of the word they are more truly pelagic than the seal or the albatross, for they never come to land, as they attach their eggs to floating debris and even the feathers of sea birds; but in another sense they are not marine insects at all, because they are never submerged. For a phytophagous insect the change from fresh water to the sea would be even more difficult, because the insect would probably have to change from eating a Phanerogam in fresh water to eating an Alga in the sea. One has to remember that in all the seas of the world there exist only about thirty species of higher plants, which belong to three genera of Hydrocharitaceæ, and five genera of Potamogetonaceæ (Arber). Therefore a phytophagous insect, unless indeed it ate diatoms in fresh water, would probably be confronted by the need of a radical change in its nutrition at the moment when it was overcoming the physical and chemical barriers to which reference has been made.

## Summary.

The habits and occurrence of a new submarine Chironomid midge (*Pontomyia natans* Edwards, described in the previous paper) which was found by the author in Samoa, are described. It is pointed out that no other insect is known which is submarine in all stages; the reason for this is obscure, in view of the great adaptability of insects to the varying conditions which prevail in fresh water. For instance, insects which live in lakes and streams are able to withstand waves and currents: larvæ of Diptera, and of one Trichopteron, can live in water as salt as or salter than the sea; among the Chironomidæ, many have marine larvæ, but in all except *Pontomyia* the adult is aerial. In estuaries, and in such seas as the Baltic and the Caspian, the boundary between fresh and salt water is gradual. In spite of this, insects have failed to colonize the sea; possibly

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they can overcome any one of the barriers which exist between fresh and salt water, but not a combination of the barriers.

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## 40. The Ossicula Auditûs of the Common Badger, *Meles taxus*. By H. C. Wilkie, F.R.C.V.S., F.R.M.S., F.Z.S.

[Received April 19, 1926: Read June 1, 1926.]

(Text-figures 1–5.)

The auditory ossicles of the Common Badger are of special interest, not only from the purely anatomical point of view, but also because it is possible to trace in their morphological characters, forms of two types, those most generally considered as belonging to the Carnivora, and some which are particularly associated with the Insectivora. These ossicles have not, so far as I am aware, been made the subject of many recorded observations.

The principal published description of them appears to be that of Doran, and this, probably owing to the extremely wide field covered by his work, is very brief. He refers to the remarkable malleus of *Meles*, its long head, the extent of its articular surfaces, and the strange conical prominence on its neck. The incus he mentions principally as being like that of the Glutton, with its far-reaching processus longus and general resemblance to the characteristic incus of the Bears.

The stapes is not referred to, nor are the ligaments and muscles connected with the ossicles. These latter have a special anatomical interest on account of their several important variations from the types most commonly found in Mammals, where such have been described, but I do not know of any recorded observations on these ligaments and muscles in *Meles*. There are consequently several gaps in the existing records which it is the object of the present notes to fill as far as possible.

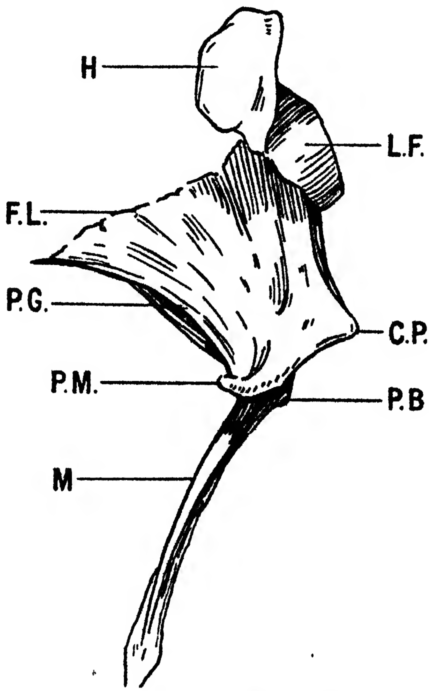
### *The Malleus.* (Text-fig. 1.)

This bone, like the other auditory ossicles of *Meles*, is relatively large in size, and has the general comparative straightness of form, and width of lamina which is common in the terrestrial Carnivora. It has, however, several strongly-marked characteristics, among which are the length of the head, the conical prominence on the posterior face of the neck, the strong and prominent processus muscularis, and the powerful well-spatulated manubrium. A vertical line drawn from the summit of the head to the terminal point of the manubrium has a measurement of 9·0 mm.

All the measurements given in these notes are those of well-developed adult male Badgers.

The upper part of the head is directed forwards, and is of globular shape anteriorly, its posterior surface being occupied by the upper articular facet, which is nearly semicircular in shape. This facet is strongly concave as to its inner half, and nearly flat as to its outer. The lower facet is long and tongue-shaped, and takes a direction downwards, and backwards. This facet has a remarkable surface, being bent slightly upwards in its middle so

Text-figure 1.




Right malleus—internal aspect.

H. Head. L.F. Lower articular facet. F.L. Free edge of lamina. P.G. Processus gracilis. C.P. Conical prominence of neck. P.M. Processus muscularis. P.B. Processus brevis. M. Manubrium.

as to form two planes, the upper of which is flat and the lower convex.

Thus the surface might be considered as consisting of two facets, and the entire articular surface of the head of the malleus, of three facets. The whole articular surface is long, measuring slightly over 3·0 mm.

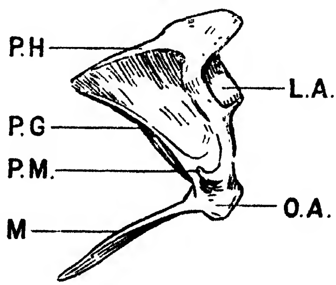
The neck of the malleus is nearly straight, and from its anterior face, and at its base, the long, thin processus gracilis

takes a sweeping curve upwards, and forwards, terminating in a fine point which joins the free edge and extremity of the lamina.

The lamina, which is of very fine bone, especially superiorly, arises from the base of the head on its *external surface*, and the free laminal margin takes a convex curvature extending downwards and forwards to join the pointed extremity of processus gracilis. United to the anterior surface of the neck on the one side the lamina joins the processus gracilis throughout its length on the other, and in doing so a ledge is formed which is of some importance, because it is upon this that the anterior ligament rests, as will be further described in dealing with the ligaments of the ossicles.

On the posterior face of the neck—and nearly on a level with the terminal point of the processus gracilis on the opposite side—

Text-figure 2.




Right malleus of *Rattus norvegicus*—internal aspect.

P.H. Prolongation of the head over the upper border of the lamina. L.A. Lower articular facet. P.G. Processus gracilis. P.M. Processus muscularis. O.A. Orbicular apophysis. M. Manubrium.

there is a long conical prominence, the signification of which has not been determined, and its exact representative has not been recorded in any other animal.

Doran considered it to be highly probable that this conical prominence is the homologue of the orbicular apophysis which exists in many of the Insectivora and the Muridæ. An orbicular apophysis has not been observed in any other of the Carnivora, and should the conical prominence be its homologue, the matter would be one of great interest in view of the known feeding habits of the Badger.

The conical prominence, although in a similar situation to the orbicular apophysis in many of the Insectivora, is placed much too high on the neck of the malleus to be in the homologous position of the well-defined orbicular apophysis in some of the Muridæ.

The position referred to is shown in text-fig 2, where the orbicular apophysis of the malleus of *Rattus norvegicus* is seen to be well down on the base of the manubrium on its inner and posterior side. A small processus brevis exists in *R. norvegicus*, but as it is on the outer surface of the base of the neck, it is hidden behind the large and well-defined orbicular apophysis.

It is important to know that the conical prominence on the Badger's malleus does not afford attachment to any ligament or tendon, and its function, if any, is quite obscure. It seems most probable that it is the trace of an ancestral form not yet determined.

The distance across the ossicle, from the point of processus gracilis to the apex of the conical process is 4·10 mm.

The processus brevis is quite rudimentary, as there is nothing but a small elevation at the root of the manubrium to represent it. This has no connection with the posterior ligament of the malleus, but on the contrary it is firmly attached to the tympanic membrane, and it is from this point to the free extremity of the manubrium that the whole attachment of the malleus to the tympanic membrane extends.

From the conical process the neck takes a sweeping curve downwards, and forwards, the continuation of which forms the processus muscularis. This latter is a strong blunt process of important size which while curving upwards, projects inwards from its base to a distance of 1·0 mm.

The base of the processus muscularis is at a distance from the summit of the head of 5·0 mm., and its distance from the free extremity of the manubrium is 4·0 mm.

The manubrium is broad laterally with two edges, an external, and an internal. The inner edge which may be said to arise from the base of the processus muscularis, is a *well-rounded* form, and from its base to its terminal point takes a double curvature, concave at first, then convex and finally slightly curves outward, its extremity becoming spatulate.

The external edge of the manubrium is *flattened*, and from its base it is at first nearly straight, then towards its extremity it becomes slightly cocave.

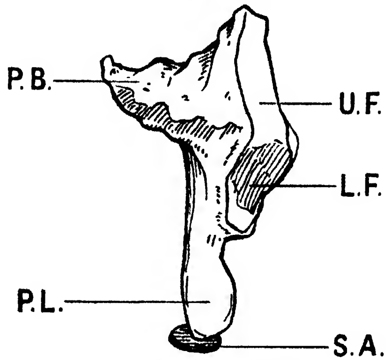
The whole of the edge is attached to the tympanic membrane, and this attachment extends from just below the upper part of the tympanal circle to well below the centre of the membrane. The vertical diameter of the tympanic membrane measures 7·0 mm., and its transverse diameter reaches nearly 8·0 mm. It is set within a strong bony frame, the tympanal circle, which is well elevated above the wall of the tympanum, especially at its lower part, where the elevation reaches 3·0 mm.

### *The Incus.* (Text-figs. 3 & 4.)

The incudes of the terrestrial Carnivora generally, so far as they have been described, appear to be nearly always rather small in proportion to the mallei.

The general rule cannot be said to be true of *Meles*, where the incus, although not relatively so large as in some of the Bovidæ, yet is of considerable volume. It has a remarkable resemblance

Text-figure 3.

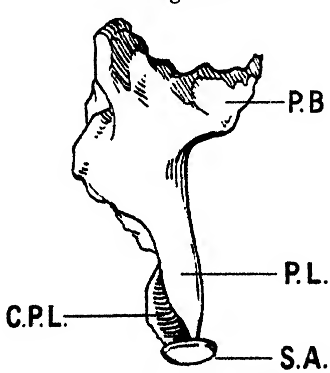



Right incus—external aspect.

P.B. Processus brevis. U.F. Upper articular facet. L.F. Lower articular facet. P.L. Processus longus. S.A. Sylvian apophysis.

to that of the Bears, on account of its long widely-divergent processus longus, and its nearly flat disc-like Sylvian apophysis.

Text-figure 4.




Right incus—internal aspect.

P.B. Processus brevis. P.L. Processus longus. C.P.L. Channel of processus longus. S.A. Sylvian apophysis.

**(This resemblance to the Bears does not extend to the malleus, as in that ossicle the processus muscularis, which is so important functionally in *Meles*, is practically obsolete in the Ursidæ.)**

The body of the incus in *Meles* is rather large and nearly square, having a long diameter of 2·20 mm. and a short one of 2·0 mm. The processus brevis is short, thick at its base, and roughly triangular in form, curving upwards at its free extremity.

The processus longus, widely divergent from the brevis, has a total length from its base to its free extremity of 2·50 mm.

The process is deeply channelled on its anterior face, a peculiarity which I think has not previously been noted in any of the Carnivora.

A channelling of the processus longus has long been recorded in certain of the Insectivora, and appears to reach its greatest development in *Talpa*, *Condylura*, and *Chrysochloris*.

Doran, referring to the processus longus of *Talpa*, says:—"It is deeply channelled on its front and *inner aspect*." This does not agree with my observations, as among the large number of moles I have examined, the position of the channelling is always on the *antero-external* aspect, and is invisible from the inner aspect of the ossicle.

In *Meles*, the channelling occupies the *anterior* face of the process and is visible from the inner side. The extremity of the process turns in a hooked form to the inner side, and to this is attached the Sylvian apophysis by a short and narrow peduncle. This apophysis is a beautiful oval disc, the long diameter of which measures nearly 1·0 mm., and it has a very slightly concave articular surface.

The peduncle, which attaches its centre to the extremity of the processus longus, is short and relatively fine. The malleo-incudal articular surface has a long diameter of rather over 3·0 mm., and the facets of the incus show even more distinctly than those of the malleus the three planes which I have described when dealing with that ossicle.

The lower facet extends well down over the base of the processus longus on its external face.

*The Stapes.* (Text-fig. 5.)

This is also a relatively large ossicle, and measures from the rim of the base to the summit of the capitulum 2·0 mm.

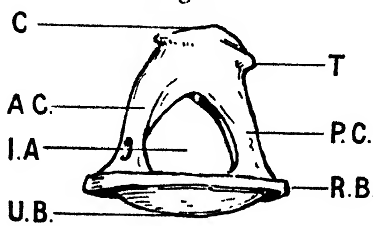
The oval base has a long diameter of 2·50 mm., and it consists of two parts, a rim of substantial thickness with square-cut edges, and a hollow well-like centre which forms a strongly-marked umbo, projecting towards the vestibule.

The crura are thick and unsymmetrical, as the posterior or shorter crus is thicker and straighter than the anterior. The capitulum is slighter convex, and is furnished with a small overhanging rim for the attachment of the capsular ligament of the joint.

The postero-internal edge of the rim inclines downwards towards the posterior crus, and expands to form a small tubercle for the insertion of the tendon of the stapedius muscle.

Beneath the capitulum the crura unite to form a bulky but hollow mass, and on this account the intercrural aperture is relatively small. This aperture, which has the form of a pointed arch, has a height from the base of 0·80 mm., and its maximum transverse diameter is about the same. The thick crura are

Text-figure 5.




Right staples—internal aspect.

C. Capitulum. T. Tubercle for insertion of stapedius tendon. A.C. Anterior crus. P.C. Posterior crus. I.A. Intercrural aperture. R.B. Rim of base. U.B. Umbo of base.

hollowed out towards the intercrural aperture, and this hollowing extends above the aperture, and below it into the bullate prominence or umbo of the base. The anterior crus is perforated by a large foramen which gives passage to the stapedial branch of the posterior tympanic artery.

*The Ligaments and Muscles.*

The ligaments and muscles of the auditory ossicles of *Meles* are in many respects especially interesting in their attachments and anatomical relationships, and I do not know of any published description of them.

*The Anterior Ligament of the Malleus.*

This arises from its attachment to the sphenoid bone, and passes through the fissura Glaseri. It becomes attached to the point of the processus gracilis and passes downwards, lying against this process and on the ledge previously described as formed by the process and the lamina.

The ligament, then passing *under* the processus muscularis, takes one complete turn round the shaft of this, and terminates in a strong insertion on its *anterior* face.

*The Posterior Ligament of the Malleus.*

This arises from a strong point of attachment to the under surface of the ridge which marks the entrance to the attic, and thence passes directly across to the processus muscularis. Passing *under* the shaft of the process it takes a complete turn round it and is finally inserted on its posterior face.

Thus both these long ligaments are *wound round* and inserted into the shaft of the processus muscularis, the anterior ligament encircling its base, and the posterior ligament winding round immediately above the anterior and at about the middle of the shaft.

Tho two ligaments form a strong sling for the malleus, and appear to obtain special strength of attachment from the manner in which each winds round the processus muscularis before arriving at its point of insertion. A remarkable disposition of the anterior ligament of the malleus occurs in *Talpa*, of which I have not seen any published description. This long ligament after passing through the fissura Glaseri, and forming a strong attachment to the free extremity of processus gracilis, follows the course of the inner lamina (for there are two in *Talpa*) as far as the groove which I described and illustrated in a former communication (P. Z. S. 1925, p. 1284).

Lodged in this groove, the ligament descends with it, and winds round the anterior face of the ossicle to gain the surface of the outer lamina, in the centre of the lower part of which there is an ovoid roughened surface, and into this the ligament is inserted.

Thus this long ligament embraces the ossicle closely by enfolding nearly its whole circumference.

There is no trace in *Talpa* of a processus muscularis.

### *The Tensor Tympani Muscle.*

This muscle in *Meles* is remarkable for its great development. It is wholly contained within the cavity of the tympanum. It arises from an extensive attachment to the roof of the tympanum, and is a large pear-shaped muscle with a maximum diameter in the uncontracted state of 3·0 mm. It terminates in a powerful tendon, which is inserted into the cap which forms the blunt free extremity of the processus muscularis.

The total length of muscle and tendon from origin to insertion is over 5·0 mm.

### *The Malleo-Incudal Capsular Ligament.*

The joint formed between the malleus and the incus is provided with a tough and rather thick capsular ligament.

A suspensory ligament with an insertion into the head of the malleus does not exist in *Meles*.

### *The Posterior Ligament of the Incus.*

This follows the course most commonly noted in other terrestrial mammals, and needs no special mention, except that it is a strong ligament of fan-shaped form, the narrow end being the insertion into the extremity of processus brevis.

*The Incudo-Stapedial Capsular Ligament.*

This is very fine in texture and loosely encloses the joint. It appears to allow very free sliding movements between the disc-like Sylvian apophysis and the facet on the capitulum of the stapes.

*The Stapedius Muscle and Tendon.*

This is a very small structure and contains but little muscular tissue. The tendon is relatively fine, and has a good point of insertion into the tubercle on the posterior and inner border of the capitulum of the stapes.

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WILKIE, H. C.—"The Auditory Apparatus of the Common Mole." Proc. Zool. Soc. London, 1925, p. 1284.

# 41. Descriptions of New Mites, including four New Species of "Red Spider." By Stanley Hirst, F.Z.S.

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(Text-figures 1–11.)

## Family Trombidiidæ.

### Parachyzeria, gen. nov.

Allied to *Chyzeria* Can. There are no processes on the body, but four large tufts of hairs are present anteriorly on the *dorsum* and also smaller whorls of hairs posteriorly. *Crista* etc. of the same type as in *Chyzeria*.

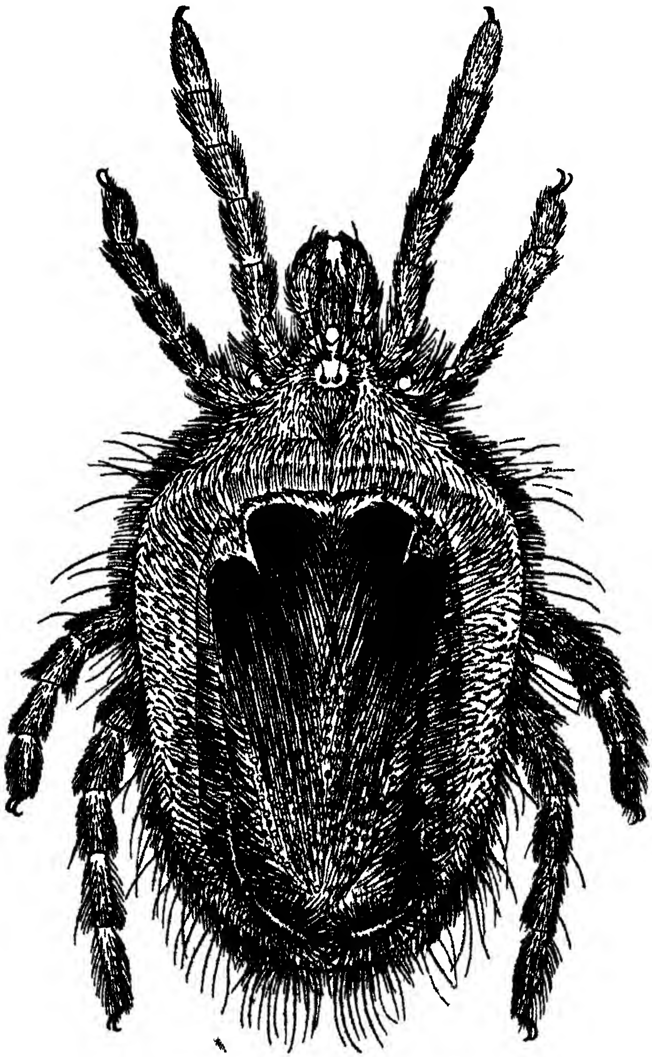
Parachyzeria indica, sp. n. (Text-fig. 1.)

♀. *Colour* (in spirit) pale yellowish to reddish, the four shoulder-tufts of hair are iridescent golden-yellow, sometimes pale copper in tint. Anteriorly there is a little median projection as in *Chyzeria novæ-zelandiæ* Hirst, but apparently more pointed; this little process seems to be part of the *crista* and bears on its base two very fine unfeathered hairs; another pair of similar very fine unfeathered hairs is present on two little rounded eye-like tubercles situated a little further back. This area supporting the crista and sensory hairs is smooth and hairless, but surrounded by a circular border of plumose hairs. A pair of *eyes* on a short peduncle is situated on each side of the *cephalothoracic part* of the *dorsum*. *Abdominal part* of *dorsum* furnished anteriorly with four conspicuous tufts of hairs; basally each tuft is very dense, consisting of two distinct kinds of hairs or setæ, viz. short, stiff, unfeathered setæ and much longer and finer plumose hairs. Near the posterior end of the body there are two (three ?) pairs of whorls also composed of two kinds of hairs, the short, stiff, plain, setiform hairs forming the centre of each whorl. Central part of abdomen dorsally furnished with numerous little circular appearances, from each of which a short and very fine stiff plain (unfeathered) hair or seta springs. Laterally there are very numerous plumose hairs, some being much longer than others. Hairs on *venter* mostly fairly short and plumose. Behind the posterior coxæ there are little smooth areas with an outer fringe of regularly-arranged stiff plumose hairs. Penultimate segment of *palp* with two strong terminal thorns, one

*Foot-note.*—With the exception of text-figs. 1 and 5, all the text-figures illustrating this paper have been done by Miss Violet Borrow with the aid of a camera lucida, under my personal supervision.

being stronger than the other; there is also a rather inconspicuous little comb composed of a few much shorter and weaker

Text-figure 1.

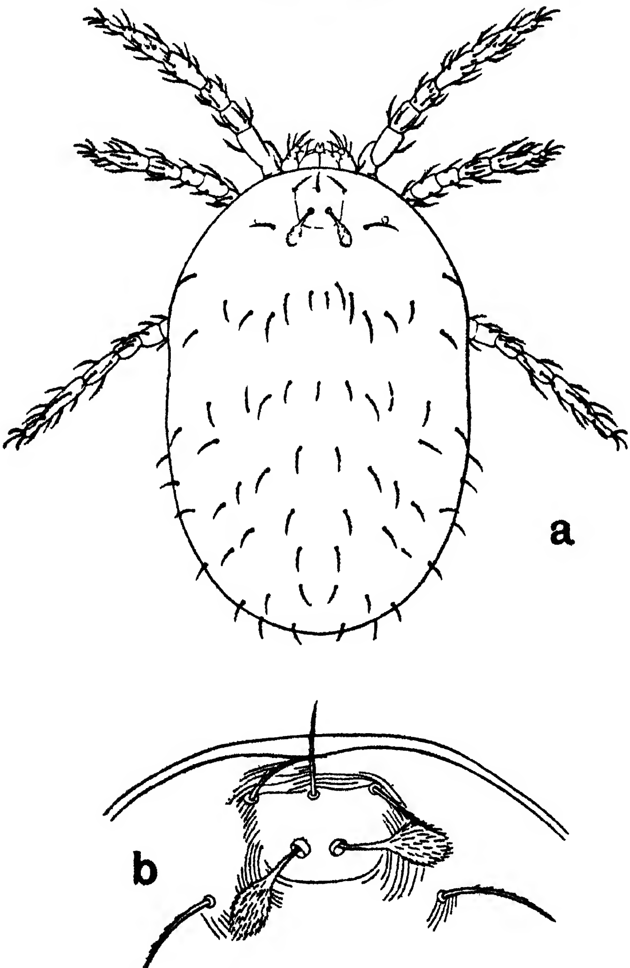


*Parachyzeria indica*, sp. n., ♀. Dorsal aspect.

setæ. Tarsus of *palp* long and slender. Besides numerous plumose hairs, the penultimate and antepenultimate segments of

the *legs* are furnished dorsally with a narrow strip of very short fine plain hairs, but this strip is restricted to the basal half of

Text-figure 2.




*Schöngastia æthiopica*, sp. n.

*a*. Dorsal aspect. *b*. The dorsal scutum greatly enlarged

the segments in the case of the second pair of legs. Claws of anterior pair of legs much smaller than those of the other legs.

*Length* of body 2·35–2·5 mm.; its greatest width (mounted specimens probably slightly pressed) 1·45–1·7 mm.

*Habitat.* India; two tubes of specimens without exact localities. One tube labelled no. 5 (M. C. Cherian) is probably from Coimbatore. The other labelled "Red Spiders on *Pistia*, 22. ix. 1921 (H. S. Rao)" probably is from Calcutta. Also a dry specimen from Bandra, Bombay (Dr. Jayakar).

SCHONGASTIA ÆTHIOPICA, sp. n. (Text-fig. 2.)

*Larval Form.—Dorsal scutum* shaped as figured (text-fig. 2 *b*); the anterior margin is very slightly sinuous; posterior margin somewhat convex; three hairs are present on the anterior margin of this scutum, one being median, the others lateral; pseudostigmal hairs placed nearer to the posterior margin than to the anterior; the enlarged distal end apparently more elongated than in *S. cercopitheci* Trgdh. The usual pair of posterior lateral hairs are not placed on the scutum. Anterior *eye* better developed than the posterior one. The integument near the eyes is rather strongly chitinized. Hairs on dorsum distributed as shown in figure; they are short and distinctly feathered. *Coxæ* each with a single feathered hair. A pair of hairs is situated between the second coxæ and another pair between the third coxæ. Hairs on posterior part of *venter* rather numerous. Hairs on dorsal surface of *palp* slightly plumose, except that on the tibia, which appears to be plain.

*Length* of body (mounted specimens, probably slightly pressed) ·43–·55 mm.

*Habitat.* Accra; on a small grey bat (Dr. Scott Macfie).

## Family TETRANYCHIDÆ.

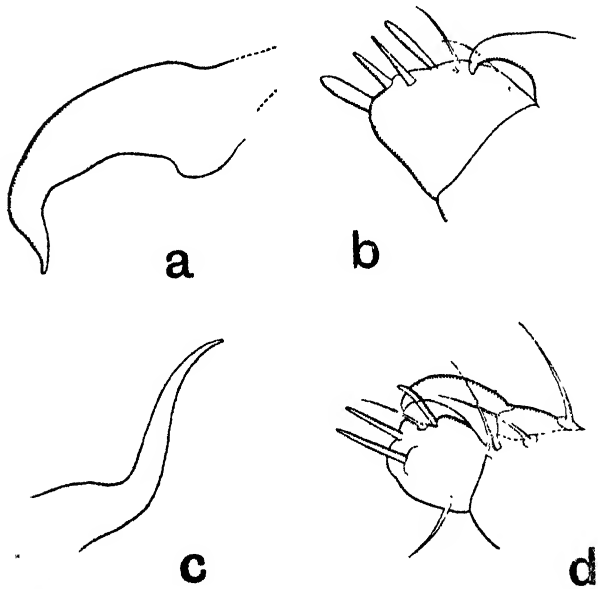
TETRANYCHUS FICI, sp. n. (Text-fig. 3 *c*, *d*.)

♂. Segmentation of *body* apparently rather distinct, three transverse lines running across the middle of the dorsum sometimes being visible, the hairs also arranged in transverse rows. Strongly-chitinized portion of *penis* fairly elongated and with a slight double sinuosity of curve resembling somewhat that of *T. carpini* Oudmns. *Terminal finger* of *palpal tarsus* either very minute or entirely absent; the two stiff terminal rod-like setæ are very long as in *T. cratægi* Hirst; *dorsal finger* fairly long, slender, slightly club-shaped. *Claw* of *first leg* rather strong and split into denticles distally much as in *T. telarius*; claws of remaining legs split into hairs as in *T. telarius*. Tenent hairs of tarsi of *legs* eight in number.

♀. *Terminal finger* of *palpal tarsus* of moderate length and stoutness; the rod-like setæ long; *dorsal finger* of palpal tarsus long and slender, being about as long as the shorter of the two, stiff, rod-like setæ. *Claws* of *legs* split into hairs distally as in *T. telarius*.

*Measurements.* Length of male (including palpi) ·29 mm., of female (incl. palpi) ·43 mm., of body of female only ·31 mm.; length of penis (strongly-chitinized protrusible portion only) 19 $\mu$, of dorsal finger of palpal tarsus of male 6 $\mu$, of rod-like

Text-figure 3.




*Tetranychus* (*Schizotetranychus*) *andropogoni*, sp. n., and *Tetranychus fici*, sp. n.
*a.* Penis of *T.* (*S.*) *andropogoni.* *b.* Palpal tarsus of *T.* (*S.*) *andropogoni*, ♂.
*c.* Penis of *T. fici.* *d.* Palpal tarsus of *T. fici*, ♂.

terminal setæ 6–6½ $\mu$, of terminal finger of palpal tarsus of female 5½ $\mu$; its width 2–3 $\mu$.

*Host plant*: Fig (*Ficus carica*), on leaves and fruit; Coimbatore, India (M. C. Cherian Coll.).

TETRANYCHUS (SCHIZOTETRANYCHUS) ANDROPOGONI, sp. n. (Text-fig. 3 *a*, *b*.)

♂. *Hairs* on *body* plain, not being feathered. *Penis* shaped rather like that of *Anychus latus* Can. & Fanz., and also somewhat resembling that of *Paratetranychus ilicis* as figured by McGregor. *Terminal finger* of *papal tarsus* moderately elongated, rather slender and bluntly pointed apically; the two rod-like setæ near the terminal finger are shorter than it; *dorsal finger* very slender and slightly club-shaped. *Claws* of all the legs *bifurcated.*

♀. *Fingers* and *setæ* on tarsus of *palp* very similar to those of the male sex. *Claws* of legs *bifurcated* as in the male.

*Length* of body of male (including head-plate) ·24 mm.; length of penis (strongly-chitinized part only) 14 μ, of terminal finger of palpal tarsus of male 5 μ, of dorsal finger of same 5 μ.

*Host plant*: *Andropogon annulatus* (leaves); Coimbatore, India (M. C. Cherian).

PARATETRANYCHUS ORYZÆ, sp. n. (Text-fig. 4 *a*, *f*, *g*.)

♂. Allied to *P. iseilemæ* Hirst, but the *penis* much better developed than in that species and more strongly curved (text-fig. 4 *f*). *Setæ* etc. of *tarsus* of *palp* very similar to those of *P. iseilemæ*; the *terminal finger* only of moderate length; *dorsal finger* about as long as the terminal finger and very slightly shorter than the longer of the two stiff rod-like setæ. *Claw* of *first leg* of male with the lower part shaped as in *P. iseilemæ* and *P. indicus*, being in the form of a single process only slightly dentate at the tip instead of split into several hair-like branches as is the case in the posterior legs. *First leg* distinctly longer than other pairs. Tenent hairs of tarsi of legs four in number.

*Length* of body (including head-plate) ·26 mm.; length of chitinous protrusible part of penis 10–13 μ, of terminal finger of palpal tarsus of male nearly 5 μ, of dorsal finger of same 5 μ, of longer of the two stiff rod-like setæ 5½ μ.

*Host plant*: Paddy (leaves); Coimbatore, India (M. C. Cherian).

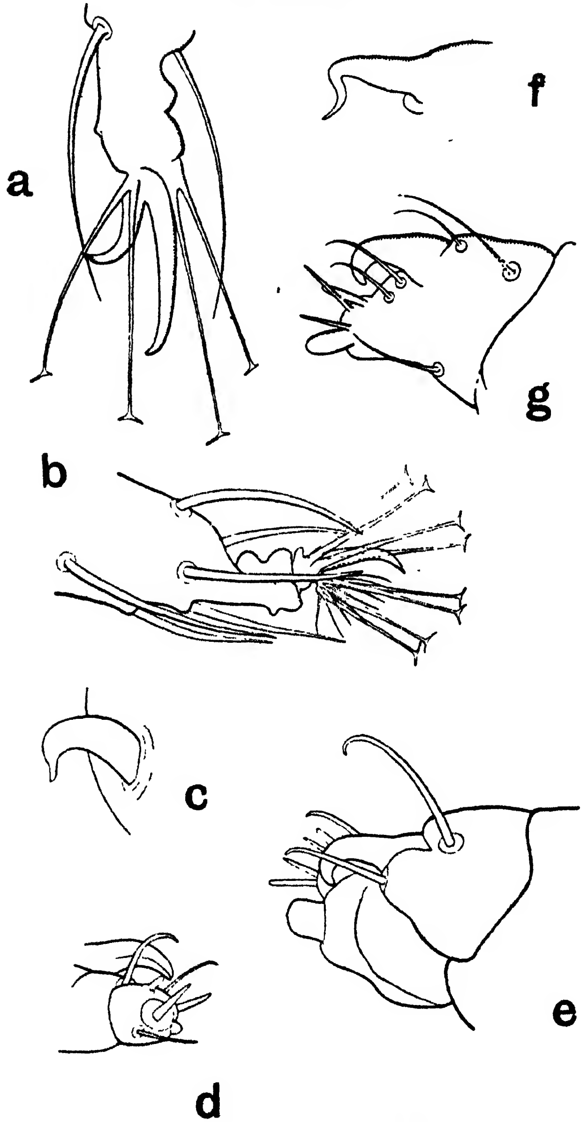
PARATETRANYCHUS PUNICÆ, sp. n. (Text-fig. 4 *b*, *c*, *d*, *e*.)

♂. *Hairs* on *body* long and densely but finely plumose. Terminal strongly-chitinized part of *penis* short, curved, the tip being narrowed and without barbs. *Setæ* on *palpal tarsus* very like those of *P. trinitatis* Hirst; *terminal finger* almost obsolete, being reduced to a small inconspicuous cone; the two stiff rod-like setæ comparatively long; *dorsal finger* unusually short. *Claws* of *legs* normal for the genus, the dorsal claw-like structure being stout, whilst the ventral part of the claw is, as usual, split into very fine hairs. Eight tenent hairs are present on the tarsus of each leg.

♀. *Terminal finger* of *palpal tarsus* in the form of a quite short but stout stump (text-fig. 4 *e*); *dorsal finger* small and slender as in the male; the shorter of the two stiff rod-like setæ distinctly longer than the terminal finger, the other rod-like seta being much longer. As in the male sex, there are eight tenent hairs at the end of the tarsi of the legs, but they are often so closely joined in pairs that they may appear to be only four in number.

*Length* of male (including palpi) ·40 mm.; length of female (including palpi) ·42 mm.; length of body-hairs of male 80–96 μ, of penis (strongly-chitinized portion only) about 11 μ, of terminal finger of male palpal tarsus 1½ μ, of dorsal finger of same 2½ μ, of stiff rod-like setæ 5–5½ μ.

Text-figure 4.




*Paratetranychus oryzæ*, sp. n., and *P. punicæ*, sp. n.

*a.* Distal end of first leg of *P. oryzæ*, ♂. *b.* Distal end of leg of *P. punicæ*. *c.* Penis of *P. punicæ*. *d.* Palpal tarsus of *P. punicæ*, ♂. *e.* Palpal tarsus of *P. punicæ*, ♀. *f.* Penis of *P. oryzæ*. *g.* Palpal tarsus of *P. oryzæ*, ♂.

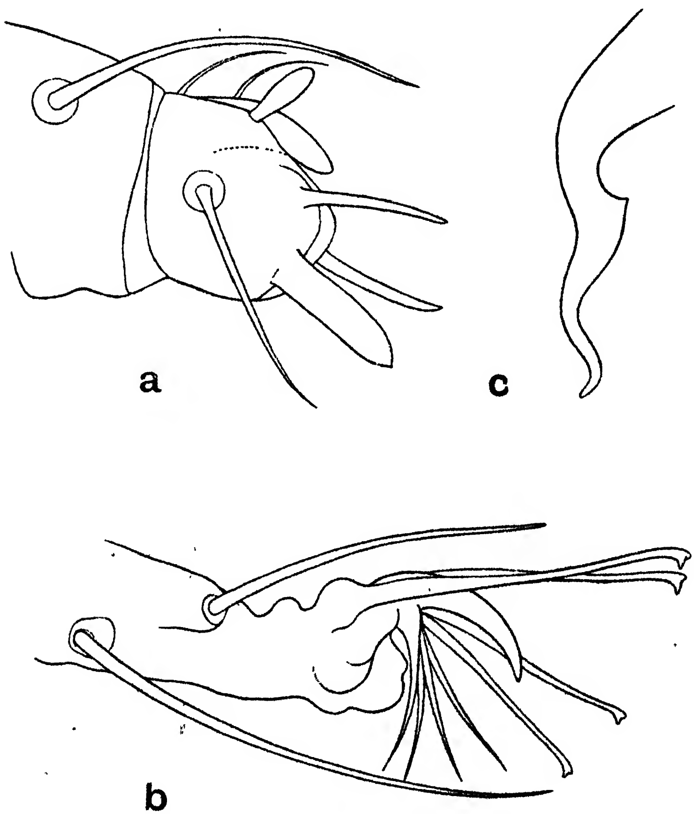
Length of terminal finger of palpal tarsus of female about $4\frac{3}{4}\,\mu$, its width $4\frac{1}{2}\,\mu$; length of dorsal finger of female palpal tarsus about $3\frac{1}{2}\,\mu$, of the stiff rod-like setæ $6$–$6\frac{1}{2}\,\mu$.

*Host plants*: Pomegranate (leaves) and grape-vine; Coimbatore, South India (M. C. Cherian).

PARATETRANYCHUS GOSSYPII Zacher. (Text-fig. 5.)

♂. *Dorsal hairs* in our specimens apparently longer and finer than the hair figured by Zacher; the basal half is not much

Text-figure 5.




*Paratetranychus gossypii* Zacher.
*a*. Palpal tarsus of male. *b*. Distal end of first leg of male. *c*. Penis.

thicker than the rest of the hair. Anterior *eye* well defined, the posterior one not so distinct. *Penis* shaped rather like that of *Tetranychus* (*Schizotetranychus*) *schizopus* Zacher, but the elongate barb much more strongly curved and the hard chitinous

part just before the barbs also more strongly curved (see text-fig. 5 *c*). *Terminal finger* of *palpal tarsus* quite long and of moderate thickness; *dorsal finger* very much shorter than the terminal finger and club-shaped; the two rod-like setæ are long and slightly curved. *Claws* of *legs* typical for the genus, having the usual undivided dorsal claw-like portion and a ventral part split into rather long fine bristles (text-fig. 5 *b*).

Note.—The tip of the *main claw* of the *palp* is truncated in the male specimen from Cassava leaves and is also slightly indented. *Dorsal finger* less club-shaped also in this specimen.

*Length* of hard chitinized portion of penis 26 $\mu$. *Terminal* finger of male palpal tarsus 9 $\mu$ in length and about 2 $\mu$ in width; dorsal finger of same 5 $\mu$ in length; longer rod-like seta 9 $\mu$ in length.

*Habitat.* Freetown, Sierra Leone; on Cassava leaves, 22. viii. 1924 (E. Hargreaves). Also Njala, Sierra Leone; on Bengal Bean, 15. v. 26 (E. Hargreaves). San Thomé, Portuguese West Africa; on *Carica papaya* (F. W. Urich).

## Family Tarsonemidæ.

Tarsonemella capensis, sp. n. (Text-figs. 6 & 7 *a*.)

♀. Closely allied to *T. africana* Hirst, but *body* apparently a little narrower. Hairs on *dorsum* very short. Distal, sensory, striated, rod-like seta of *first tarsus* (text-fig. 7 *a*) shorter and stouter than in *T. africana*; the two more proximal striated setæ on this tarsus are very slender, one being longer than the other and slightly club shaped. *Second* and *third legs* with pulvillus, but the *fourth* is modified as in *Tarsonemus*, being narrowed and furnished with the usual terminal seta. Tarsus of *second leg* with a short stout seta externally and also a slender, fairly elongate, striated, rod-like seta.

*Length* of body (including capitulum) 200–203 $\mu$; its width 90 $\mu$.

*Hab.* Mossel Bay, Cape Province, South Africa; several specimens on *Alfonsiella* sp. (R. E. Turner).

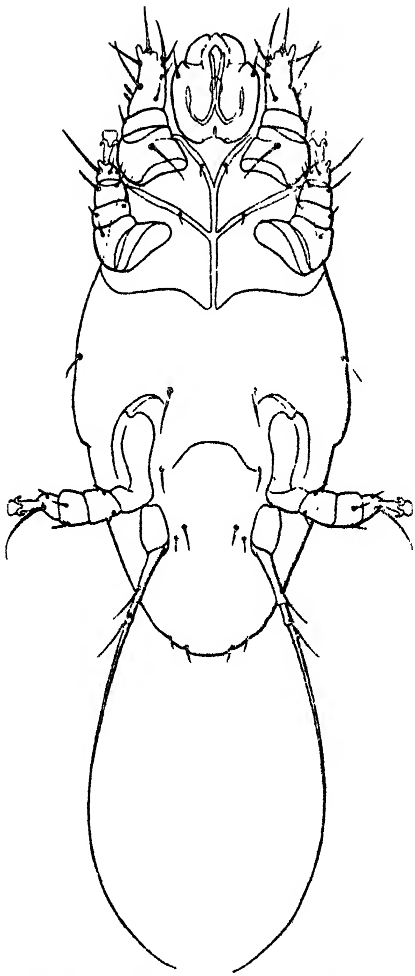
## Family Sarcoptidæ.

Chorioptes texanus Hirst. (Text-fig. 7 *b*.)

I take the opportunity to publish a drawing of the posterior lobe of the male of this species, showing the shape and length of the setæ etc. It will be seen that the setæ on this lobe differ greatly from those present in the same position in *Chorioptes equi* var. *capræ* Gerv. & Bened. Flattened blade-like hairs on the abdominal lobes very much narrower than in *C. equi* var. *capræ*. Outermost hair of each lobe quite short and fine, whereas in the var. *capræ* this hair is very long and also thickened at the base. Feet in both sexes of *C. texanus* normal for the genus

*Chorioptes*, the stalk bearing the sucker being short and unsegmented. It will be seen from the above that two quite

Text-figure 6.



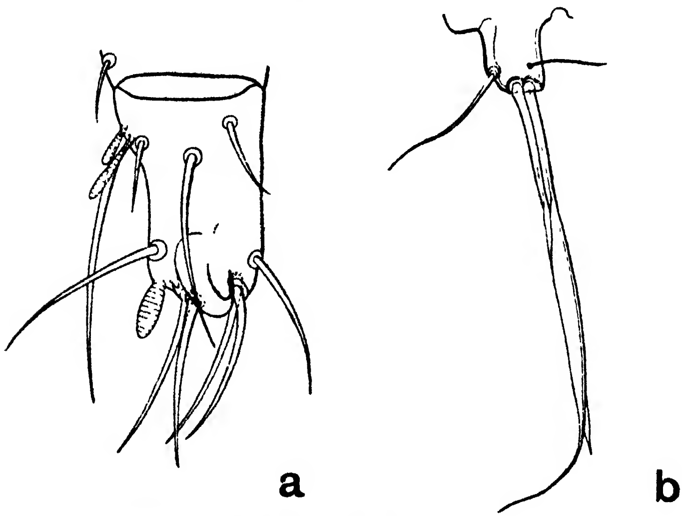
*Tarsonemella capensis*, sp. n., ♀. Ventral aspect.

distinct species of the genus *Chorioptes* are to be found parasitic on goats.

NOTE.—Since writing the above my attention has been directed to a paper recently published by Oudemans, entitled " *Chorioptes*

*capræ* Del. & Bourg. 1858" (Tijdschr. Ent. 1926, lxix. pp. 1–18, 4 pls.). In this paper Oudemans describes at length specimens of a *Chorioptes* taken on goats at Buitenzorg, Java. This *Chorioptes* certainly seems to be the same as the one I have described under the name *C. texanus*, but there is no real

Text-figure 7.




*a. Tarsonemella capensis*, sp. n. Tarsus of first leg.
*b. Chorioptes texanus* Hirst. Abdominal lobe of male, showing setæ.

evidence to show that it is *C. capræ*. In his great work on medical zoology, Railliet, who has examined Delafond's types of *C. capræ*, regards it as a variety of *C. equi*. I myself have seen and studied quite typical specimens of *C. equi* found on goats.

## Family GAMASIDÆ.

### LIPONYSSUS SUDANENSIS, sp. n.

♀. Closely allied to *L. nyassæ* mihi and to *L. chiropteralis* mihi, having two dorsal shields as in those species, but the second and third coxæ each have a short, strong, pointed spur ventrally, whereas in the two species just mentioned there are no ventral spurs on the coxæ. *Dorsal shields* shaped as in *L. chiropteralis*; the posterior shield has three pairs of comparatively long hairs on its surface and two or three pairs of very short hairs at the posterior end (sometimes there is a pair of longer hairs posteriorly). Hairs on rest of *dorsum* fine

and stiff and fairly numerous. *Sternal plate* very much wider than long; three pairs of hairs are present on this plate, the posterior pair being placed on its much thickened concave posterior margin. *Genito-ventral plate* normal for the genus, being wedge-shaped and furnished with the usual pair of hairs; posteriorly it ends in an unusually fine point; surface of this plate posteriorly with two strong linear markings converging near the middle to form a single line. First and fourth *coxæ* without any spur; second coxa with an anterior spur dorsally and with a short but strong, pointed, ventral spur; third coxa with a similar ventral spur. *Anal plate* normal, being pear-shaped and with the three usual hairs. *Peritremal tube* reaching forwards almost to the anterior end of the second coxa. First free segment of *palp* with a distinct ventral process. *Legs* furnished with fine hairs.

*Length* of body ·63–·70 mm.; its width ·38–·40 mm.

*Habitat.* Khartoum, Sudan; off Bat (*Liponycteris nudiventris*), 9. xii. 1925 (H. B. Johnston).

NEOLÆLAPS, subgen. nov.

*Peritremal tube* unusually wide. *Genito-ventral plate* with only three pairs of hairs. Other characters as in *Lælaps* (s. s.).

LÆLAPS (NEOLÆLAPS) MAGNISTIGMATUS (Vitzthum). (Text-fig. 8.)

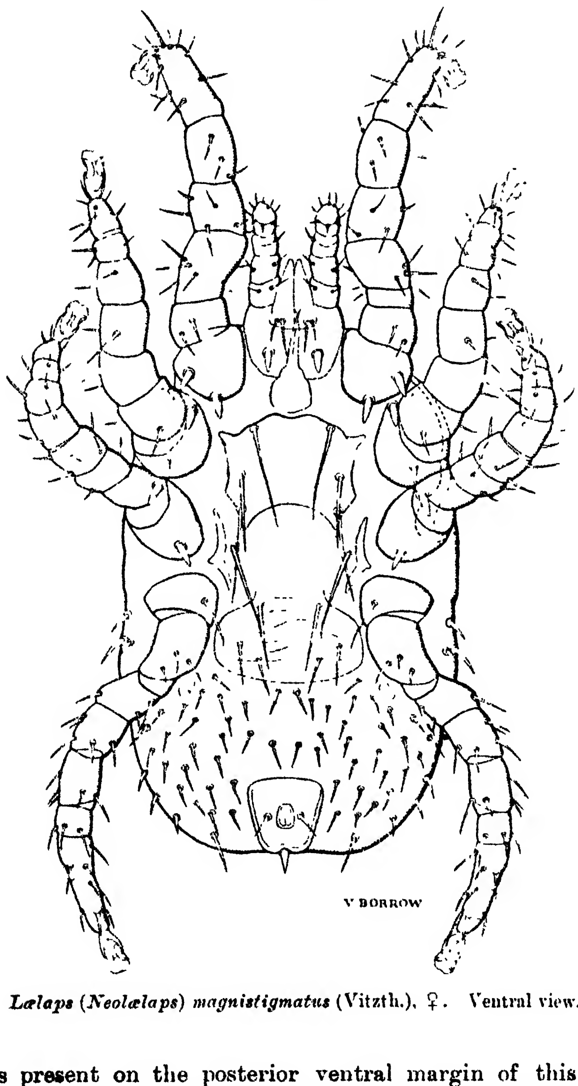
*Liponyssus magnistigmatus* Vitzth. Arch. Naturg., Abt. A, lxxxiv. 1918, pp. 21–23, text-figs. 14 & 15; id. Treubia, viii. 1926, pp. 93–104, text-figs. 58–65.

? LEIOGNATHUS SPINOSUS, Berlese, Redia, vi. 1910, p. 261.

♀. *Dorsal shield* covering the entire dorsum, but slightly narrowed near the middle at the posterior end of the peritremal tube; hairs on this shield rather numerous, one or two of the posterior hairs being longer than the others. *Sternal plate* shaped as shown in figure, the posterior margin being concave; it has faint rather scale-like or reticulate markings on its surface; the three pairs of hairs on this plate are long. *Genito-ventral plate* short but wide, being shaped as figured; there are only three pairs of hairs on this plate (instead of four pairs as in typical *Lælaps*); very faint linear markings like those present in *L. nuttalli* etc. are visible on the surface. Posterior unpaired hair on the *anal plate* much stouter than the paired hairs, all three hairs being short. Hairs on the *venter* short and fine, but there is a longer posterior hair on each side of the anal plate. *Peritremal tube* unusually large and wide, the posterior end of it being swollen and bulbous; the tubular part reaches anteriorly just beyond the anterior surface of the second coxa. On each side of the ventral surface of the *capitulum* there is a stout thorn as in *L. parvulus* Hirst. Coxa of first *leg* with a pair of stout

thorns, and second coxa with a dorsal thorn anteriorly as in some species of *Liponyssus*, besides a ventral anterior thorn; only a

Text-figure 8.




*Lælaps* (*Neolælaps*) *magnistigmatus* (Vitzth.), ♀. Ventral view.

seta is present on the posterior ventral margin of this coxa. Third coxa with a rather thin antero-ventral thorn and a shorter thorn on its posterior margin. Last coxa unarmed.

*Length* of body ·56–·60 mm.

*Hab.* Kalutara, Ceylon; specimens from *Pteropus giganteus*, received through Mr. H. Scott. Kuching, Sarawak; specimens from *Pteropus edule* (J. Hewitt).

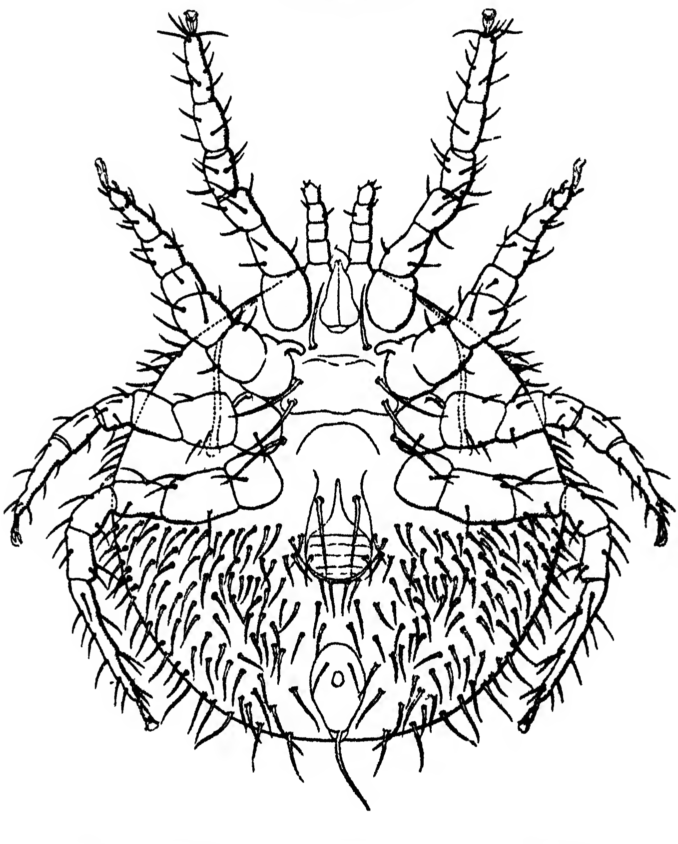
HETEROLÆLAPS, subgen. nov.

*Genito-ventral plate* very small and furnished with five pairs of hairs. Second and third coxæ each with a ventral spur.

LÆLAPS (HETEROLÆLAPS) ANTIPODIANA, sp. n. (Text-fig. 9.)

♀. Rather a wide species, the width being only a little less than the length. Hairs on *dorsal scutum* longer but much less

Text-figure 9.

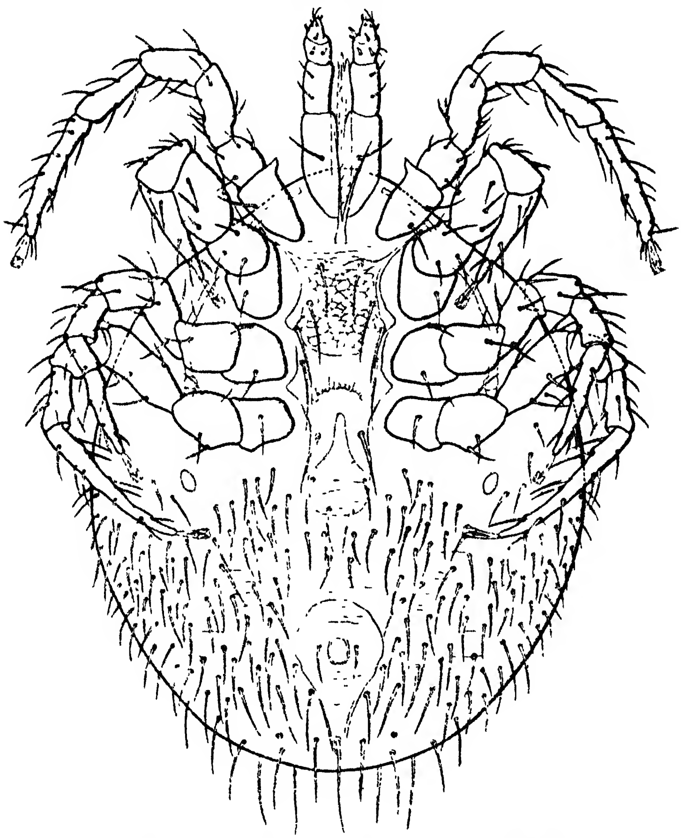


*Lælaps (Heterolælaps) antipodiana*, sp. n., ♀. Ventral view.

numerous than those on the sides and venter. *Sternal plate* trapezoidal, the posterior margin being straight, its surface

furnished with faint reticulate markings; it has three pairs of hairs, the two posterior pairs being long. *Genito-ventral plate* resembling that of *L. anomalus* in its small size, but not sac-shaped, having straighter sides; this plate is provided with very fine indistinct linear markings very like those present in *L. nuttalli* etc.; there are usually five pairs of hairs on this plate,

Text-figure 10.



*Lælaps (Mesolælaps) anomalus*, sp. n., ♀. Ventral view.

the anterior pair being unusually long; the posterior pairs of hairs are placed on the margin and apparently vary in number. *Anal plate* not very large, being shaped as figured; it is narrower than that of *L. anomalus*. *Venter* densely furnished with rather stout hairs; posteriorly these hairs are longer and slightly plumose. *Peritremal tube* extending as far forwards as the second

coxa or beyond it. Second coxa with a compressed, blunt, stump-like spur and a similar but much smaller spur is present also on the third coxa.

*Length* of body ·87–·96 mm.; its greatest width about ·73–·85 mm.

*Habitat.* Sydney, Australia; on *Perameles nasuta* (Molteno Institute of Parasitology).

MESOLÆLAPS, subgen. nov.

*Genito-ventral plate* very small, sac-shaped in outline, and with only three pairs of hairs. *Coxæ* without spurs. *Peritremal tube* not enlarged.

LÆLAPS (MESOLÆLAPS) ANOMALUS, sp. n. (Text-fig. 10.)

♀. *Dorsal scutum* elongate-oval, about one and a half times longer than wide; it is slightly wider behind the last pair of legs than anteriorly; hairs on its surface fairly long, especially the posterior ones. Hairs on lateral uncovered part of *dorsum* very numerous and shorter than those on the scutum, but posteriorly on this uncovered part there are some longer hairs. *Sternal plate* fairly large and shaped as figured, the posterior margin being convex; its surface is ornamented with a network of linear markings; three pairs of hairs are present on this plate. *Genito-ventral plate* sac-shaped, but very much smaller than is usually the case in the genus *Lælaps* and with only three pairs of hairs; it has linear markings mostly transverse in direction as in *Lælaps nuttalli* etc. *Anal plate* large and pear-shaped, the pointed posterior end being somewhat elongated; anteriorly this plate is marked with curved parallel striations. *Coxal platelet* elongate but not very narrow. *Peritremal tube* long, extending forwards beyond the first coxa. Hairs on *venter* numerous and not very long except at the posterior end of the body; some of them are slightly plumose. *Legs* slender and furnished with fine hairs, mostly slightly plumose.

*Measurements.* Length of body 1·06 mm.

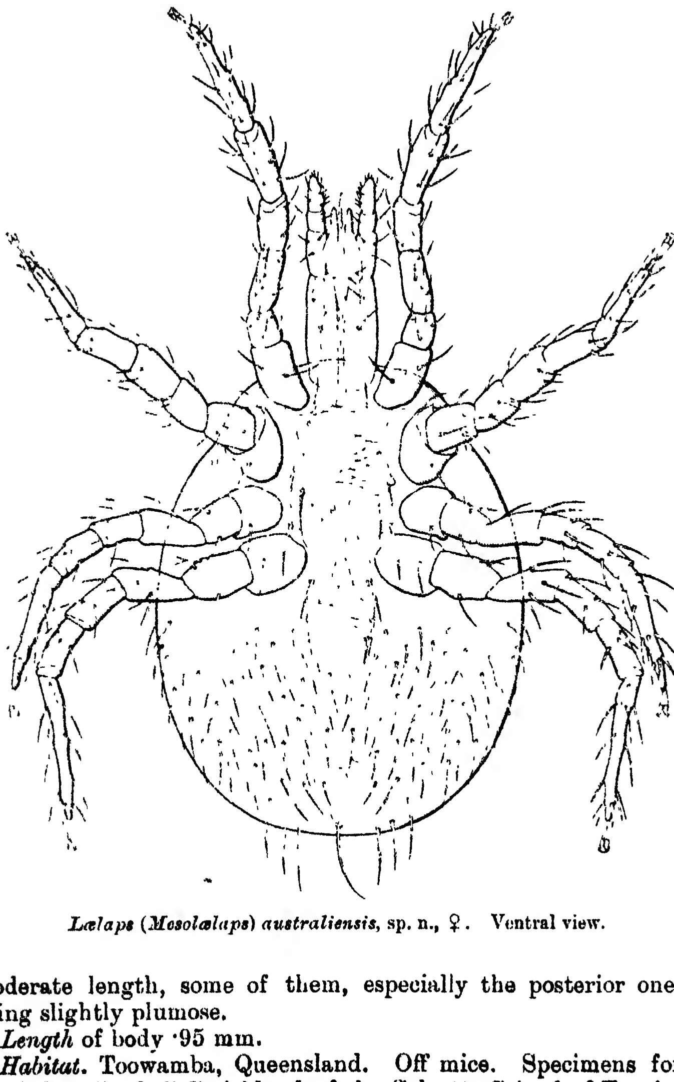
*Habitat.* Sattelberg, Huon Gulf, New Guinea; *Perameles*, 1911 (Prof. F. Foster).

LÆLAPS (MESOLÆLAPS) AUSTRALIENSIS, sp. n. (Text-fig. 11.)

♀. Allied to *Lælaps* (*Mesolælaps*) *anomalus*, sp. n., having only three pairs of hairs on the genito-ventral plate as in that species, but this plate is larger in *L. australiensis*. *Dorsal scutum* elongate-oval. *Sternal plate* well developed, reticulate, and with the three usual pairs of hairs; its posterior margin is concave (that of *L. anomalus* is distincly convex). *Genito-ventral plate* with only three pairs of hairs; it is ornamented with transverse linear markings as in *L. nuttalli* etc. *Anal plate* moderately well developed but smaller than that of *L. anomalus*; it is fairly

wide and the three hairs are fairly long, especially the posterior unpaired hair. *Coxal platelet* comma-shaped. *Peritremal tube* long, reaching forwards to join that of the opposite side of the body and being fused with it. Hairs on *venter* numerous and of

Text-figure 11.



*Lælaps* (*Mesolælaps*) *australiensis*, sp. n., ♀. Ventral view.

moderate length, some of them, especially the posterior ones, being slightly plumose.

*Length* of body ·95 mm.

*Habitat.* Toowamba, Queensland. Off mice. Specimens forwarded by Prof. C. Strickland, of the Calcutta School of Tropical Medicine.

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GROWTH CHANGES IN THE SKULL OF THE BABOON *Papio porcarius.*

# 42. Growth-changes in the Skull of the Baboon, *Papio porcarius* *. By S. Zuckerman, M.A.†

[Received April 16, 1926: Read June 1, 1926.]

(Plate I.‡; Text-figures 1–7.)

## (1) Introduction.

The growth changes in any skull after birth are very striking. For example, Froriep, in the early part of the nineteenth century, pointed out that in the case of the human skull, the size of the cranium of the new-born infant is eight times that of the face; whereas in the adult the cranium is only twice the bulk of the face. Much more striking changes take place in the post-natal development of the skulls of other primates, such as the Gorilla, Chimpanzee, etc.

Bischoff (1867) published a detailed account of the growth-changes in the Orang, Chimpanzee, and Gorilla. Since his time there does not appear to have been published any other account which deals with all the growth-changes in any one species. Virchow (1880), Topinard (1867), amongst others have also contributed to this study. Of recent workers may be mentioned Bolk, Duckworth (1915), and, more particularly, Keith (1895, 1910, 1925).

Complete references were not available during the course of this investigation, but I have been able to ascertain the more important results of most of the work which has been done in this field. In most cases only isolated aspects of the various growth phenomena have been dealt with, and the literature on the subject is very scattered.

So far as I have been able to discover, no work of this nature has been done on the Baboon skull. Accordingly, at Professor M. R. Drennan's suggestion, I undertook to investigate the growth-changes on the material at my disposal in Cape Town. The importance of such investigations for the proper interpretation of young primate skulls cannot be exaggerated.

## (2) Material and Acknowledgments.

The material available for this study in Cape Town consists of forty skulls, all belonging to the same species, and probably also to the same variety of Baboon, i. e., *Papio porcarius*. So far as I have been able to ascertain, all have come from the region south of the Karroo—the southern districts of the Cape Province.

* Being a research undertaken while working for the Degree of Master of Arts in Anatomy, at the University of Cape Town.

† Communicated by Prof. G. Elliot Smith, F.R.S., F.Z.S.

‡ For explanation of the Plate see page 873.

Twenty-six skulls, in better condition than the others, were selected for more intensive study. Detailed measurements, etc. of these skulls are given in Table I. Of these twenty-six skulls, fourteen belonged to the Anatomical Department of the University of Cape Town, six to the Zoological Department, and six to the South African Museum.

I wish to express my indebtedness to Dr. C. von Bonde, of the Zoological Department of the University of Cape Town, and to Dr. Gill, of the South African Museum, for access to their material.

## (3) General Considerations.

### (*a*) Ageing of the Skulls.

In the literature dealing with the Baboon there is no information concerning the dates at which the various teeth erupt, nor have I been able to get much further information on this point from naturalists who are interested in these animals. The only reliable information which I have is derived from personal observations on a young male Baboon, born in captivity, whose age is thus definitely known. When twelve months old he began to cut his first permanent lower molars, and now, at the age of thirteen months, his first permanent upper molars have appeared.

As a further point of interest in this connection it may be mentioned that, when on a hunting expedition, I secured a full-grown aged male (B. 17), an immature lactating female (B. 8), whose third molars had not yet erupted, and her male baby (B. 1) with two median milk incisors in both jaws, and with the metopic suture fully open. The latter animal could not have been more than a few weeks old. (Bryce, 'Quain's Anatomy,' 1915, vol. iv. p. 61, states that in the Anthropoid Apes fusion of the metopic suture occurs either before or just after birth.)

Owing to this scarcity of reliable information as regards the ageing of baboons, I have contented myself with arranging the skulls in a series according to the stage of dentition presented by each. After dentition is complete the arranging of the skulls in order of age becomes much more difficult, but by careful attention to the various criteria of maturity—such as are used in estimating the age of a human skull—an attempt has been made to prolong the series upwards.

Table I. contains detailed measurements of the twenty-six skulls selected for more intensive study. These skulls have been arranged in order of age, and the sex is indicated.

In the case of the skulls which possessed a complete permanent dentition (B. 9–B. 12 in the adult female group, and M. 4–B. 19 in the adult male group in Table I.), the criteria of age which were chiefly consulted were (1) the condition of the spheno-basilar suture, (2) the condition of the other cranial sutures,

(3) the condition of the teeth, and (4) the development of the crests, although not much reliance was placed on this factor.

In skulls M. 4 to B. 18 in Table I. the spheno-basilar suture is unclosed, though all except M. 4 evince signs of being in the adult condition (Duckworth, 1904, 'Studies in Anthropology,' records the same occurrence in the Gorilla). The order in which the skulls of this sub-group have been placed was decided upon after a thorough examination of the degree of closure of this suture and after consideration of the other criteria mentioned above. B. 9 in the female group also exhibited patency of this suture.

Skulls B. 15 and B. 16 in the male group and B. 10 and B. 11 in the female present the merest indication of the line of fusion of the constituent bones. Skulls B. 17, M. 6, B. 19 in the male group and Z. 1 and B. 12 in the female group have the synostosis complete. All other criteria substantiate the order in which the skulls have been arranged.

### (*b*) Sexing of the Skulls.

This is an easy task in the case of those skulls which possess complete permanent dentition. The adult male skull is distinguished from the female by the possession of (1) enlarged canine teeth, often reaching 50 mm. in length, (2) by the development of sagittal and occipital crests, and (3) mainly by the size of the whole skull. The average prosthion-inion diameter in the case of the male is well over 210 mm., and in the female this measurement seldom rises above 180 mm. In the case of the younger skulls, especially of those with milk dentition, the differentiation of the sexes is by no means simple. Fortunately, with regard to these, definite information was obtained as to the sex of the skulls.

## (4) Growth-changes in the Skull.

### (*a*) General.

(1) *Growth of the Skull as a whole.*

Of the anthropoid skull Keith (1910) writes: "The vast changes which occur in the skull after birth are due mainly to three factors: (1) eruption of the teeth and increase of the jaws to accommodate the increased dentition, (2) the growth of the muscles of mastication and especially of their area of origin from the cranium, and (3) modification of the nuchal area of the skull."

It will be shown that in the case of the Baboon a considerable increase in the cranium, which takes place during the period of eruption of the permanent teeth, is an additional factor in the growth of the skull which cannot be ignored, however much it may be overshadowed by the other factors.

TABLE I. (Part 1.)

| Number of skull. | Description of skull. | 1. Prosthion-inion length. | 2. Maximum ant. post. diameter. | 3. Maximum transverse diameter. | 4. Basion-bregma height. | 5. Auriculo-bregmatic height. | 6. Minimum frontal breadth. | 7. Maximum bi-mastoid width. | 8. Maximum bi-zygomatic width. |
|---|---|---|---|---|---|---|---|---|---|
| B. 1. | Metopic suture patent. Only median milk incisors erupted in both jaws. ♂. | 95 | 78·5 | 61·5 | 48·5 | 45 | 45 | 51 | 54 |
| B. 2 | Complete milk dentition. ♀. | 120 | 98 | 74 | 57 | 52 | 52 | 74 | 7[illegible] |
| B. 3 | Ditto. 1st perm. molars appearing. ♂. | 127 | 100 | 76 | 62·5 | 53 | 19 | 78 | 8[illegible] |
| B. 4 | Perm. 1st molar and median incisors erupted, lat incisors appearing. ♂. | 140 | 10[illegible] | 78 | 62 | 57 | 55 | 79 | 8[illegible] |
| B. 5 | Slightly older than B. 4, same stage of dent. ♂. | 145 | — | 80 | — | 56 | 58·5 | 78 | 8[illegible] |
| B. 6. | 2nd premolars erupting. 3rd M. and canines absent. ♀. | 161 | 107 | 78 | 67 | 53 | 54 | 79 | 9[illegible] |
| B. 7. | Perm canines erupting. ♂. | 161 | 110 | 78 | 71 | 59 | 53 | 80 | 9[illegible] |
| B. 8 | 3rd molar erupting in lower jaw. ♀. | 155 | 103 | 76 | 67 | 52 | 52 | 76 | 9[illegible] |
| B. 9. | 3rd M. newly erupted Open bas.-sphen suture. ♀. | 166·5 | 109 | 76 | 67 | 52 | 55 | 83 | 10[illegible] |
| B. 10. | ♀ adult. Indication of B. S. suture | 172 | 109 | 76 | 66 | 53 | 52 | 79 | 9[illegible] |
| B. 11. | ♀ adult. Indication of B. S. suture | 172 | 109 | 79 | 68 | 52 | 51 | 84 | 10[illegible] |
| Z. 1. | ♀ adult. Fused B. S. suture. | 175 | 110 | 77·5 | 67 | 52 | 52·5 | 80 | 9[illegible] |
| B. 12. | ♀ adult. Fused B. S. suture. | 181 | 108 | 80·5 | 66 | 54 | 52 | 82 | 105 |
| M. 4. | Sub-adult ♂ canines 30 mm. Open basi-sphenoid suture. | 208 | 114 | 80 | 70 | 54 | 51 | 96 | 117 |
| M. 7. | Adult ♂ C. 43 mm. Open basi-sphenoid suture. | 208 | 115 | 78 | 79 | 56 | 51 | 87 | 11[illegible] |
| B. 13. | Adult ♂ C. absent. Open basi-sphenoid suture. | 210 | 115·5 | 82 | 70 | 50 | 57 | 97 | 114 |
| B. 14. | Adult ♂ C. absent. Open basi-sphenoid suture. | 211 | 115 | 85 | 71 | 54 | 56 | 95 | 117 |
| M. 5. | Adult ♂ C. 42 mm. Open basi-sphenoid suture. | 217 | 121 | 84 | 76 | 56·5 | 54 | 94 | 118 |
| Z. 2. | Adult ♂ C. 49 mm. Open basi-sphenoid suture. | 220 | 123 | 87 | 77 | 62 | 59 | 100 | 130 |
| Z. 3. | Adult ♂ C. 39 mm. Open basi-sphenoid suture. | 221 | 120 | 83 | 74 | 56 | 58 | 96 | — |
| B. 18. | Adult ♂ C. 49 mm. Open basi-sphenoid suture. | 225 | 120 | 82 | 73 | 54 | 50 | 93 | 117 |
| B. 15 | Adult ♂ C. 45 mm. Almost fused B.S. suture. | 215 | 117 | 82 | 74 | 58 | 59 | 89 | — |
| B. 16 | Adult ♂ C. absent. Almost fused B.S. suture. | 220 | 117 | 86·5 | 77 | 56 | 56 | — | — |
| B. 17. | Adult ♂ C. 46 mm. Almost fused B.S. suture. | 224 | 122 | 86 | 76 | 58 | — | 109 | 122 |
| M. 6. | Adult ♂ C. 43 mm. Fused B.S. suture. | 235 | 122 | 87 | 75 | 59 | 59 | 98 | 131 |
| B. 19. | Adult ♂ C. 51 mm. Fused B.S. suture. | 239 | 120 | 82 | 73 | 58 | 55 | 91 | 118 |

TABLE I. (Part 2.)

| 9. Naso-basion length. | 10. Basion-prosthion length. | 11. Naso-menton length. | 12. Naso-prosthion length. | 13. Nasal height. | 14. Breadth U. alveolar border. | 15. Length U. alveolar arch. | 16. Length palate. | 17. Breadth palate. | 18. Orbital alveolar height. | 19. Bicondylar width. | 20. Vomer basion length. | 21. Cranial capacity. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 45 | 51 | 45 | 31 | 30 | 28 | 28 | 23 | 16 | 15 | 46 | 17 | 108 c.c. |
| 60 | 70 | — | 49 | 46 | 38 | 44 | 37 | 21 | 25 | — | 20 | 166 5 c.c. |
| 66 | 77 | 81 | 56 5 | 54 | 40 | 45 | 41 | 21 | 26 | 71 | 21 | 174 c.c. |
| 67 | 91 | — | 70 | 67 | 44 | 56 | 46 | 23 | 33 | — | 22 | 182·5 c.c. |
| — | — | 90 | 63 | 59 | 45 | 55 | 45 | 24 | 32 | 75 | — | — |
| 78 | 113 | 96 5 | 83 | 77 | 50 | 70 | 68 | 27 | 36 | 83 | 26 | 173·5 c.c |
| 77 | 111 | 108 | 80 | 73 | 49 | 68 | 62 | 25 | 38 | 85 | 26 | 186·5 c.c |
| 72 | 104 | 103 | 83 | 77 | 48 | 65 | 58 | 26 | 38 | 82 | 25 5 | 168 c.c. |
| 76·5 | 118 | 112 | 92 | 85 | 47 | 76 | 65 | 24 | 38 | 88 | 27 | 171·5 c.c. |
| 79 | 121 | — | 98 | 90 | 46 | 77 | 67 | 25 | 47 | — | 28 | 176·5 c.c. |
| 80 | 123·5 | — | 103·5 | 95 | 50 | 81 5 | 74 | 27 | 47 | — | 28·5 | 183·5 c.c. |
| 79 | 122 5 | — | 99 | 90 | 47 | 80 | 74 | 27 | 44 | — | 28 | 171·5 c.c. |
| 80 | 132 | 129 | 108 | 94 | 51 | 83 | 73 | 25 | 50 | 92 | 29 | 181·5 c.c. |
| 85 | 150 | 147 | 129 | 120 | 52 | 97 | 91 | 30 | 55 | 94 | 29 | 198 5 c.c. |
| 89 | 149 | 151 | 130 | 115 | 54 | 96 | 89 | 30 | 51 | 94 | 29 | 191·5 c.c |
| 92 | 151 | — | 130 | 123 | 54 | 97 | 89 | 31 | 57 | — | 30 | 193·5 c.c. |
| 90 | 154 | — | 134 | 125 | 55 | 100 | 91 | 29·5 | 54 | — | 31 | 206·5 c.c. |
| 99 | 160 | 157 | 135 | 119 | 56·5 | 100 | 93·5 | 33 | 62 | 100 | 35 | 231·5 c.c. |
| 94 | 161 | 167 | 143 | 127 | 57 | 102 | 100 | 31 | 65 | 107 | 31·5 | 216·5 c.c. |
| 91 | 161 | 163 | 145 | 127 | 55 | 107 | 100 | 31·5 | 64 | 101 | 32·5 | 191·5 c.c. |
| 94 | 160 | 167 | 141 | 131 | 54·5 | 105 | 95 | 30 | 57 | 91 | 33·5 | 206·5 c.c |
| 95 | 158 | 163 | 140 | 130 | 54 | 97 | 96 | 28 | 60 | 93 | 34 | 211·5 c.c. |
| 96 | 160 5 | — | 133 | 123 | 56 | 100 | 92 | 31 | 57 | — | 33·5 | 216·5 c.c. |
| 93 | 160 | 162 | 145 | 127 | 57 | 104 | 96 | 34 | 66 | 102 | 32·5 | 232·5 c.c. |
| 96 | 169 | 180 | 159 | 140 | 56 | 110 | 104 | 30 | 68 | 107 | 36·5 | 216·5 c.c. |
| 94 | 174 | 174 | 156 | 138 | 55 | 110 | 104 | 29 | 61 | — | 34·5 | 201·5 c.c. |

*Prosthion-inion diameter.*

Having arranged the skulls in order of age and according to sex, it is interesting to find that the prosthion-inion diameter increases progressively throughout the series. Reference to Table I. shows that the only skulls deviating from this rule are B 15, B. 16, and B. 17, a degree of deviation which is normally to be expected in any series of skulls.

The gradual increase in size throughout the series is due mainly to the forward extension of the muzzle during growth, as shown by the increase in the basion-prosthion diameter. There are, however, other growth factors which concern the increase in length of the skull, such as the increase in the antero-posterior diameter of the cranium, and the increase in area of the nuchal plane, which will be referred to later on.

The average prosthion-inion diameter during milk dentition is 124 mm. In the adult female it is 173 mm., an increase of 40 per cent. In the adult male the average is 220 mm., an increase of 78 per cent. The increase in this diameter from the skull B. 7, representing a stage when the male Baboon cuts its permanent canines—the third molars being as yet unerupted,—to the average diameter for the adult male is 36 per cent. From B. 8, the stage when the female cuts its third molars, to the average diameter for adult females the increase is 11·6 per cent.

For what length of time the process of elongation of the skull continues it is difficult to state. FitzSimons (1919, 1924) gives the average longevity of Baboons as fifty years, and the end of growth about twenty. My results seem to show that a certain amount of growth takes place throughout life, as has been found to be the case in the skull of the Orang (Keith, 1896; Sonntag, 1924).

I have, therefore, come to the following conclusions: (1) that Baboon skulls can be roughly aged relative to the prosthion-inion diameter, and (2) that the process of growth, particularly of the muzzle, proceeds for a considerable time after all the permanent teeth have erupted.

(2) *Proportion of Face to Cranium at various Growth-stages.*

There is nothing more striking in the growth of the skull, as shown in Pl. I. and text-fig. 1, than the remarkable changes which occur in the relative proportions of the facial and the cranial skeletons. Text-fig. 1 shows profile and basal views, originally drawn on squared millimetre paper, of skulls B. 1, a skull at birth, B. 2 at the stage of the completed milk dentition, B. 11 an adult female, and B. 17 and B. 15, adult males.

By counting the number of squares antero-inferior and supero-posterior to the basion-nasion line which represents the basi-cranial axis, the proportions of face to cranium in the case of each skull may be estimated. This gives the ratio of the area of the face to that of the cranium on median sagittal sections of

F. P. Stowell, B.Sc., Ph.D., A.I.C., Aquarium Research Fellow.

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P. CHALMERS MITCHELL,

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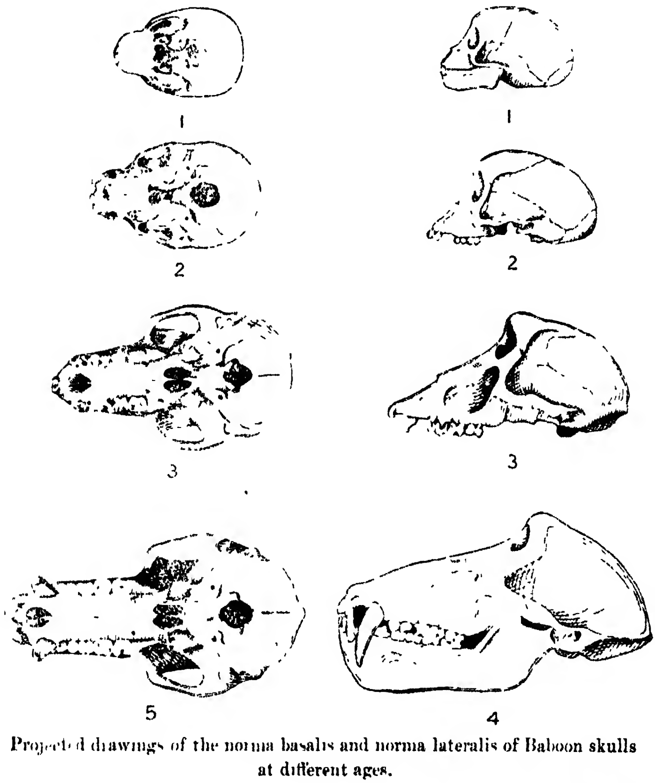
*November 23rd*, 1926.

the skulls. (The basion-nasion line, of course, cuts off a portion of the middle cranial fossa from the cranial part posterior; but this amount is regarded as being balanced from the point of view of actual cranial capacity by the large amount of upward bulging of the orbital plates.)

Text-figure 1.




Projected drawings of the norma basalis and norma lateralis of Baboon skulls at different ages.

1=Skull just after birth (B. 1); 2=Skull with milk dentition (B. 2); 3=Adult female (B. 11); 4=Adult male (B. 17); 5=Adult male (B. 15).

In this manner these proportions were assessed in twelve skulls, and the average proportions in the case of skulls without the mandibles are as follows:—

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| At birth ................ | Face | : | Cranium | :: | 1 | : | $3\frac{1}{2}$ |
| During milk dentition. | „ | : | „ | :: | 1 | : | $2\frac{1}{2}$ |
| Adult female ............ | „ | : | „ | :: | 1 | : | 1 |
| Adult male.. ............ | „ | : | „ | :: | 2 | : | 1 |

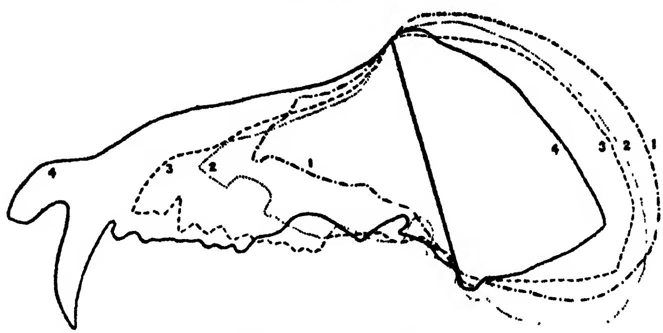
When the mandibles are included, the proportions of face to

cranium at the different stages of growth become considerably altered:—

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| At birth .................. | Face | : | Cranium | : : | 1 | : | $2\frac{1}{2}$ |
| During milk dentition . | ,, | : | ,, | : : | 1 | : | $1\frac{1}{4}$ |
| Adult female ............ | ,, | : | ,, | : : | $1\frac{1}{2}$ | : | 1 |
| Adult male ... .......... | ,, | : | ,, | : : | $2\frac{1}{2}$ | : | 1 |

To emphasise these changes text-fig. 2 has been prepared by superimposing, by means of the epidiascope, projected profile views of skulls B. 1, B. 2, B. 8, and B. 19 on a common basi-cranial axis. All except B. 8 are male skulls.

Text-figure 2.




Profile view of four Baboon skulls at different ages, superimposed on a common Nasion-basion line, to show the gradual increase in prognathism, and the relative diminution of the cranium as age advances.

1=Skull just after birth (B. 1); 2=Skull with milk dentition (B. 2); 3=Subadult female (B. 8); 4=Adult male (B. 19).

This diagram shows in a striking manner the gradual increase in the projection of the face and the relative diminution in the size of the cranium as age advances.

### (b) Cranium.

(1) *Sutural Occlusion.*

It is a well-known fact that in the higher anthropoids—the Gorilla and Orang, for instance—occlusion of the cranial sutures occurs comparatively early in life, *i. e.*, at or soon after the attainment of a complete set of permanent teeth. This synostosis is probably due more to the development of the sagittal and occipital crests than to anything else. The adult Gibbon skull has patent sutures.

In the Baboon the condition of the sutures is midway between that of the Gibbon and that of the higher anthropoids. The adult female Baboon corresponds with the adult Gibbon in that in her case sagittal and occipital crests are never developed. The sutures in the female Baboon remain patent throughout life, for

in no female skull examined were the sagittal, lambdoidal, or coronal sutures obliterated.

In the male the sutures remain open, without doubt, as late as the completion of the permanent dentition. In all the mature male skulls examined the coronal suture is patent. The sagittal suture is evident in some, in others it is occluded by the development of the sagittal crest. The bregma can always be accurately defined. The lambdoid suture is very indistinct in all adult male skulls. In some skulls, it and the lambda have become obliterated by the development of the occipital crest and external occipital protuberance. The more usual condition, however, appears to be one in which the lambdoid suture is situated about 5 mm. above the occipital crest, while the lambda is found in the posterior part of the sagittal crest. The asterion, in both male and female adult skulls, is situated on the ridge formed by the union of the posterior root of the zygoma and the occipital crest. In younger skulls it is found on the point of union of the posterior root of the zygoma and the supreme nuchal line. This is noteworthy, for it implies that the asterion can be regarded as a relatively stationary point during the growth of the skull. As such it is of value in marking out the sub-cerebral plane on a projected view of a skull (Keith, 1925).

The metopic suture is quite patent in B. 1. No indication of it was seen in any other skull (see p. 844).

(2) *Cephalic Index.*

Measurements show that the Baboon skull during youth borders on the brachycephalic type, but with increasing age, both in male and female, it tends to become dolichocephalic. In taking the cranial measurements the external muscular crests were included. Hartmann and Virchow (1885) record the same occurrence in the Gorilla. The inion in young skulls lies well below the lambda, but in older skulls the inion ascends, until in the mature male both points are close together. In the mature female the lambda is always situated about 10 mm. above the external occipital protuberance.

The greatest transverse diameter is found in younger skulls (milk dentition) on the parietal bone or parieto-squamous suture. In both sexes, as the skull grows, the greatest transverse diameter descends, and soon it is found on the junction of the squamous temporal with the posterior root of the zygoma.

(3) *Supraorbital Ridges.*

The supraorbital ridges are never completely joined across the nose as they are in the Gorilla, and are relatively small. They attain their greatest development in the male, and their main growth appears to take place after all the teeth have erupted.

(4) *Temporal Lines.*

At birth (B. 1) the squamous temporal barely forms one-quarter of the lateral wall of the cranium above the root of the

zygoma. As the skull ages, this amount increases until it forms at least a third. This is due to the slight amount of growth which occurs in the parietal bones after milk dentition. This will be referred to later.

At birth and in very young skulls the temporal lines are situated almost 10 mm. above the inferior border of the parietal bone. During milk dentition they are found from 15 to 20 mm. above the same level. In the adult female the temporal lines never come nearer the mid-line than 10 mm. The final condition of the temporal lines in the adult male corresponds closely in appearance to the condition found in the adult female Gorilla. The temporal lines of each side meet each other posteriorly in the region of the external occipital protuberance. Posterolaterally, they fuse with the supreme nuchal line to form the occipital crests. In the median plane posteriorly they fuse with each other and the occipital crest to form a very prominent external occipital protuberance. In better-developed skulls a sagittal crest is formed by the fusion of the two temporal lines in the mid-line above. This crest may extend forward to within 1 cm. from the bregma, and it may attain a height posteriorly of almost 10 mm.

(5) *Temporal Fossæ.*

The depth of the temporal fossæ is measured by the difference between the maximum bi-zygomatic width and a minimum diameter of the cranium taken on the floor of the temporal fossa. This latter measurement was taken on the frontal-alisphenoid articulation in the temporal fossa (Table I. col. 6). There is practically no increase in this latter dimension of the skull after milk dentition, little more than 1 mm. separating the width in the skulls of milk dentition, adult females, and adult males. On the other hand, the bi-zygomatic width at birth (B. 1) is 54 mm. During milk dentition the average width is 76 mm., an increase during the first period of growth of 41 per cent. In the adult female the average width is 100 mm., an increase of 33 per cent. relative to the width during milk dentition. In the adult male the average width is 120 mm., an increase of 58 per cent.

At birth the depth of the fossa as defined above is 9 mm. During milk dentition it is 25 mm., in the adult female 47 mm., and in the adult male the depth is 65 mm.

(6) *Occipital Plane and Nuchal Plane.*

The occipital crests assume their final positions much sooner than do the temporal, which appear to meet each other posteriorly only after the eruption of all the permanent teeth. At the commencement of milk dentition the planum nuchale and planum occipitale are about equal in size. On the attainment of complete milk dentition the latter is about one-third the size of the planum nuchale. In both sexes before the attainment of a complete permanent dentition—soon after the canines are erupted—the occipital crests have almost reached their highest point (B. 7 and

B. 8). In the female no further change occurs after this stage; but in the male the temporal crests extend upwards and posteriorly, and, as described above, fuse with the occipital crests posteriorly and with each other in the median line above.

The modification in the planum nuchale is due to factors similar to those which operate in the Gorilla and other anthropoids (Keith, 1910): viz., an increased area for firmer muscular attachment of the skull to the trunk is required, and this allows for better use of the enlarged jaws. During milk dentition the height of the planum nuchale is 25 mm., measured from the opisthion to its superior border, in the adult female it is 33 mm., and in the adult male 43 mm. The increase in height of the nuchal area relative to the condition during milk dentition is to the extent of 33 per cent. in the female and 75 per cent. in the male. The increase in width of the nuchal area will be discussed in connection with the bi-mastoid breadth in the next section.

(7) *Increase in the Breadth of the Base of the Skull.*

This can be observed from the increase in the bi-condylar width of the mandible in Table I.

At birth (B. 1) the breadth of the base of the skull measures 46 mm. During milk dentition it is 71 mm., an increase of 54 per cent. The average in the adult female is 90 mm., the percentage increase relative to the width during milk dentition being 27. In the adult male the average bi-condylar width is 99 mm., and the increase 40 per cent., due, of course, to the greater development of the masticatory function.

The increase in the bi-mastoid width demonstrates both the growth at the base of the skull and also the increase in breadth of the nuchal area. In a sense it shows the increase in the width of the base of the brain-box far better than does the bi-condylar measurement. For, as the skull advances in age, the glenoid cavity comes to lie relatively more lateral to the margin of the cranium proper than it does in younger skulls. This is due to the bowing-out of the zygomatic arch, which also accounts for the increase in depth of the temporal fossa. The root of the zygomatic arch joins the base of the cranium as a broad thick plate, flattened from above downwards. In adult skulls, on the inferior aspect of the root, quite two-thirds of the area of the glenoid fossa will be found lateral to the cranium proper, while in skulls of milk dentition not one-third occupies this position.

The bi-mastoid width was taken on the widest part of the mastoid portion of the temporals directly posterior to the external acoustic meatus. The position of this point corresponds to that of the mastoid process in the higher anthropoids. In the Baboon, however, the true mastoid processes lie directly below the tympanic bone, directed downwards and forwards. At birth the bi-mastoid width is 51 mm. (B. 1). During milk dentition the average is 76 mm., an increase of 50 per cent. In the adult female the average is 82 mm., an increase of but 8 per cent.

relative to the width during milk dentition. In the adult male the average width is 95 mm., an increase of 25 per cent.

The points used in taking this bi-mastoid width are more prominent in the male. a fact correlated with its stronger musculature. Their prominence is chiefly due to the subjacent mastoid air-cells. Air-cells have the effect of decreasing the weight of the bone, and are more developed throughout the skull of the adult male, with its prominent crests and ridges, than they are in the female or the growing skull. No large air-sinuses are to be found anywhere in the Baboon skull; for example, there is no frontal sinus and no maxillary sinus.

(8) *Growth-changes in the Shape of the Occipital Condyles.*

In skulls of milk dentition the condyles are more or less flat, and are directed chiefly downwards. The poise of the head on the vertebral column alters during the eruption of the permanent teeth and with the increase in size of the masticatory apparatus. The alteration is due to the pushing forwards of the face relative to the condyles to allow for the free play of the enlarged mandible. In accordance, then, with the firmer poise of the head, it is not surprising to find that the articular surfaces of the condyles are directed laterally as the skull ages, and, further, that the condyles become bent on themselves, presenting a large antero-lateral surface, and a smaller surface which is directed more or less posteriorly. All these features assist in the firmer support of the skull.

## (c) Face.

(1) *Growth-changes in the Basi-cranial Axis.*

(a) *General.*

The growth of the Baboon skull conforms to the general rules which govern the growth-changes in the basi-cranial axis, in the plane of the foramen magnum, and in the spheno-ethmoidal angle of Mammals. More especially does it agree with the higher anthropoids in this respect. It must be borne in mind, however, that no increase in the endo-cranial cavity is stated to occur after the period of milk dentition in the higher anthropoids (Keith, Bolk, etc.). Such an increase will be shown, on the other hand, to occur in the case of the Baboon. This fact, therefore, modifies the usual description (Keith and others) of the process of growth in the basi-cranial axis in the Gorilla and the rest of the anthropoids.

Briefly summarised, the growth-changes in the basi-cranial axis of the Gorilla are as follows (Keith, 1910; Duckworth, 1915) :—(1) After birth and until the brain-case ceases to enlarge, the tendency is for the anterior limb of the basi-cranial axis—the plane of the cribriform plate—to be depressed. The spheno-ethmoidal angle (angle between prosphenion-nasion and prosphenion-basion lines) thus decreases in size. (2) Growth of

the brain in the posterior aspect of the skull opens out the foramino-basal angle (angle between the basion-opisthion and basion-prosphenion lines). (3) The process of "correction," by which the plane of the foramen magnum is altered and the foramino-basal angle becomes smaller, sets in with the eruption of the permanent teeth and the growth of the masticatory muscles. This "correction" is due to (*a*) the growth of the basilar plate pushing the face forwards relative to the occipital condyles (or the condyles backwards relative to the face), and to (*b*) the displacement of the opisthion as a result of the extension and upward growth of the nuchal area.

As far as the Baboon is concerned, the gorilloid process of backward migration of the occipital condyles and consequent decrease in the foramino-basal angle during the process of "correction" takes place. In Table I., col. 20, is given the length in each skull of the basilar plate measured from the basion to the most posterior point of articulation of the vomer with the basi-sphenoid. At birth (B. 1) the length of the basilar plate is 17 mm., while during milk dentition the average length is 20·5 mm., an increase of 20 per cent. during the period of eruption of the milk teeth. The average length in adult females is 28 mm., an increase of 37 per cent. relative to the length during the milk dentition. In the adult male the average is 33 mm., an increase of 61 per cent.

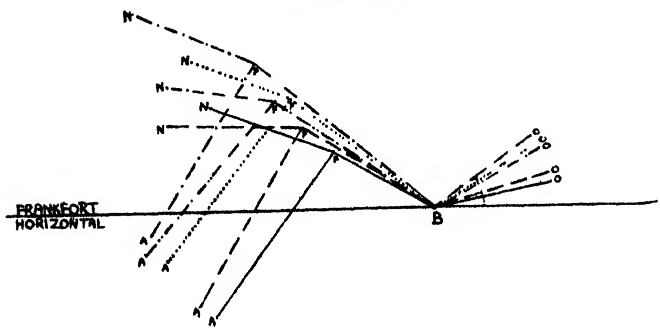
Further investigation in connection with these changes was made on nine skulls bisected in the median sagittal plane. The following table contains the information gained from these sections:—

TABLE II.

| | B. 1. | B. 3. | B. 4 | B. 7 | B. 8. | B. 10. | B. 11 | B. 13. | B. 17 | B. 14 |
|---|---|---|---|---|---|---|---|---|---|---|
| Foramino-basal angle (plane of foramen magnum to basi-cranial axis) | 139° | 131 | 132·5 | 119 | 113·5° | 114 | 125° | 110 | 106° | — |
| Inclination of plane of foramen magnum to Frankfort plane. | 11° | 15° | 11° | 27 | 27·5° | 31° | 25° | 30° | 36° | — |
| Spheno-ethmoidal angle, measured to nasion. | 165° | 150° | 157·5° | 146° | 150° | 160° | 157° | 153° | 157° | — |
| Spheno-ethmoidal angle, measured to frontal point. | 175° | 150° | 157·5° | 156° | 155° | 168·5° | 167° | 162·5° | 168° | — |
| Spheno-maxillary angle. | 97·5° | 90° | 92·5° | 96·5° | 88° | 92° | 90° | 85° | 83° | — |
| Prosphenion-basion length (mm.). | 31 | 42 | 41 | 52 | 45·5 | 50 | 52 | 66·5 | 61 | 61 |

The gradual decrease in the size of the foramino-basal angle as the skull ages is well shown in Table II. as well as the varying

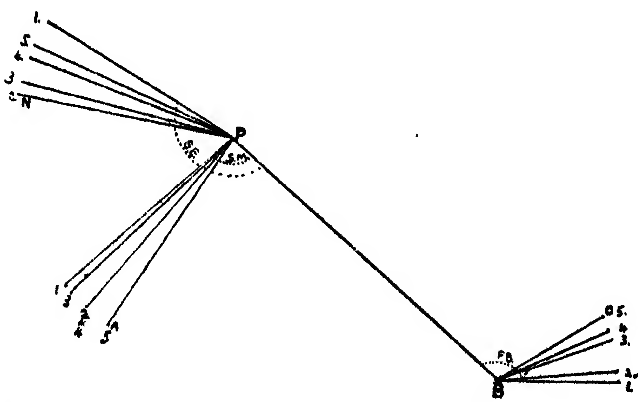
Text-figure 3.




The basicranial axis, spheno-maxillary, spheno-ethmoidal, and foramino-basal angles at different stages of growth. The varying angle of inclination of the plane of the foramen magnum, B-O, to the Frankfort Horizontal is shown.

B=Basion; O=Opisthion; N=Nasion; P=Prosphenion; A=Prosthion. Undivided line=B. 1 (birth); Punctuated line=Milk Dentition. Dash, double dot line=B. 7 Stage during eruption of permanent teeth. Dotted line=Adult female. Dash-dot line=Adult male.

Text-figure 4.




Changes in the Foramino-basal (F.B.), spheno-maxillary (S.M.), spheno-ethmoidal (S.E.) angles during growth. A common prosphenion-basion line is employed.

P=Prosphenion; N=Nasion; B=Basion; O=Opisthion; A=Prosthion; 1=Skull at birth; 2=Milk dentition; 3=B. 7 (as in text-fig. 3); 4=Adult female; 5=Adult male.

inclination of the plane of the foramen magnum to the Frankfort Horizontal. Text-figs. 3 and 4 have been prepared to demonstrate these two points.

A note on the measuring of the cranial and facial angles in the Baboon is here called for. The methods followed in obtaining the values of these angles are those indicated in Duckworth's 'Morphology and Anthropology' (1904); but, owing to the fact that these values do not quite agree with the usual ones attributed to the Baboon, it seems desirable to give the details of the procedure followed.

Such points as the nasion, opisthion, basion, and prosthion obviously need not be discussed, but the prosphenion, owing to a peculiar pattern of the bones in the anterior cranial fossa in the Baboon, requires special mention. The prosphenion was taken as that point in the anterior cranial fossa where the presphenoid bone articulates with the frontal bone in the mid-line. There is in the Baboon a conformation of the bones in the anterior cranial fossa similar to the conformation found in the African Simiidæ, the Chimpanzee and Gorilla. That is to say, in the Baboon the presphenoid is separated from the ethmoid by "flange-like" processes of the frontal, the ethmoid being much reduced in size. The same point is used as the prosphenion in the Gorilla and Chimpanzee, and it is from this point that bending of the anterior limb of the basi-cranial axis occurs.

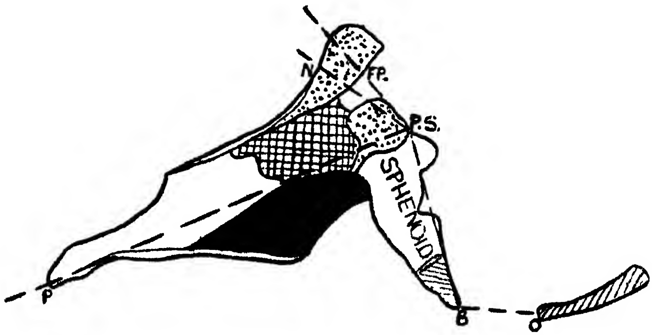
In detailing the procedure for obtaining the spheno-ethmoidal angle, Duckworth mentions the fact that in human skulls the foramen cæcum is a much more truthful point to use in representing the bending of the anterior limb of the basi-cranial axis than the nasion. The latter is, however, the more standardised point for the anterior limit of the anterior limb.

On the Baboon skull the nasion does not correspond in all cases to the anterior limit of the anterior limb of the basi-cranial axis. A more useful point for this purpose is one which may be called the "Frontal Point." This point is the anterior limit of the brim of the small pit found in the anterior part of the floor of the anterior cranial fossa. The ethmoid is suppressed to such an extent in the Baboon that the cribriform plate barely exists. Text-fig. 5 demonstrates the axis and the points used. It is an actual tracing of the median sagittal section of skull B. 8. Pl. I. also shows four such skulls, with the various points indicated (B. 4, B. 3, B. 11, and B. 17).

The angles were measured on tracings of the various skulls (*cf.* text-fig. 5), and they were verified on the actual sagittal sections themselves. In this way no loophole was left for error, and yet the values of the angles obtained by these methods do not correspond to the values generally assigned to Cercopithecidæ. For instance, the average value of the foramino-basal angle for adult Baboons is 114°, which is not far removed from 120°, quoted by Duckworth for the Simiidæ. Further, the spheno-ethmoidal angle measured at the nasion has a value in adult

Baboon skulls of 157°, and measured at the "frontal point" (Table II.) it is 166°. This amount of depression of the anterior base is said by Duckworth to occur in the Gorilla and Chimpanzee.

Text-figure 5.




Tracing of sagittal section of skull B. 8. The nasion (N) has been moved downwards slightly to emphasise the line P.S.–F.P. (Prosphenion to "Frontal Point").

B = Basion; O = Opisthion; P = Prosthion. Stippled area = Frontal; Crossed area = Ethmoid; Black area = Vomer; Lined area = Occipital.

Yet the value of the spheno-ethmoidal angle in the Baboon is generally assumed to be midway between the values in the anthropoids and those of the Dog, for which latter Duckworth gives 231°.

(b) *Growth-changes in the Foramino-basal Angle.*

It has been mentioned already that the changes in the size of this angle during growth are of the same nature as those in the skulls of higher anthropoids. There is no evidence, however, in the present material of a preliminary opening-out of the foramino-basal angle during brain-growth (see text-figs. 3 and 4).

The foramino-basal angle gradually decreases in size, the most rapid change taking place, as indicated in Table II., during the period of eruption of the permanent teeth (B. 4, B. 7, and B. 8.).

The angle of inclination of the plane of the foramen magnum, or posterior base, to the posterior arm of the Frankfort Horizontal gradually increases with age (see text-fig. 3).

(c) *Growth-changes in the Spheno-ethmoidal Angle.*

This angle varies very greatly in the series studied. At birth the angle is greatest, *i.e.*, the anterior base is least depressed (B. 1, 175°). During milk dentition it is at its lowest value (B. 3, 150°), and thereafter it increases again until it assumes

the value of 166° in adult skulls This latter change is due to the various changes in the basi-cranial axis and spheno-maxillary angle which will be referred to now.

(2) *Spheno-maxillary Angle and Prognathism.*

(a) *General.*

In the case of this angle most unexpected results were obtained. The average value of this angle in all the skulls bisected was 90° 30′, the average value for adult males in this group being 84°. These figures form a striking contrast to the values of this angle given by Duckworth (1904) in the following table:—

Cercopithecus Monkey, 119°.
Simia, 146°.
Gorilla, 125°.
Chimpanzee, 121°.
Aboriginals of Australia, 92° 20′.
Europeans, 75° 30′.

It is not stated whether the Cercopithecus Monkey was a Baboon or not. The value of the spheno-maxillary angle measured from a Baboon skull figured in Duckworth's 'Morphology and Anthropology' is in the region of 105°, so that even this figure, although 10° or so above the figure I have given, is less than the value for the Chimpanzee.

The point to be noticed is that the value which I have secured for the spheno-maxillary angle in the Baboon falls far below the values in the Simiidæ, and even below the values for Australian aboriginals. I have been unable to find any other record of the value of this angle for the Baboon skull. References made to it, as can be seen from the quotations from Huxley and Gregory given below, imply that it is much greater than in any other primate skull.

The value of the spheno-maxillary angle lies in the fact that it represents a measure of the inclination of the facial axis to the basi-cranial axis. The diverse views which exist as to the amount of this inclination in the Gorilla and Baboon are exemplified by the following two passages.

Huxley (1863) wrote as follows:—"The difference between a Gorilla and a Baboon is even greater than appears at first sight; for the great facial mass of the former is largely due to a downward development of the jaws, an essentially human character, superadded upon that almost purely forward, essentially brutal development of the same part which characterises the Baboon."

Gregory (1922) explained the form of the Gorilla skull in this manner:—"The head is lengthened by the forward growth of the muzzle and by the extreme backward growth of the skull-top. Thus the Gorilla skull, to a certain extent, parallels that of the Baboons."

There does not appear, therefore, judging from these statements, to be any certain knowledge of facial growth either in the

Baboon or Gorilla. The idea common to both statements, however, is that the face of the Baboon is an essentially forward development.

On the other hand, I have shown that the inclination of the facial axis to the basi-cranial axis in the Baboon is definitely less than in the anthropoids, and in the case of adult males is within the range of values given for the human skull.

Now, the Baboon is the most prognathous of the primates. In the face of the results which I have obtained it is extremely doubtful whether the spheno-maxillary angle can be considered as a measure of prognathism, and still less as "the most important angular measurement by which prognathism can be represented" (Duckworth, 1904). It merely represents the inclination of the facial to the basi-cranial axis.

If it were the only criterion of prognathism, then the Baboon would be definitely less prognathous than the higher Simiidæ—a conclusion which would be absurd.

(b) *Age-changes in the Spheno-maxillary Angle.*

Reference to Table II. shows that at birth (B. 1) it is greatest—97° 30′. During milk dentition and the period of eruption of the permanent teeth it ranges between this value and 90°. The average value for adult females is 91° (B. 10 and B. 11), and for adult males it is 84° (B. 13 and B. 17). Verification tests made on projected profile views of other Baboon skulls not included in the table, in which the position of the prosphenion was calculated, demonstrated the same decrease in this angle during growth.

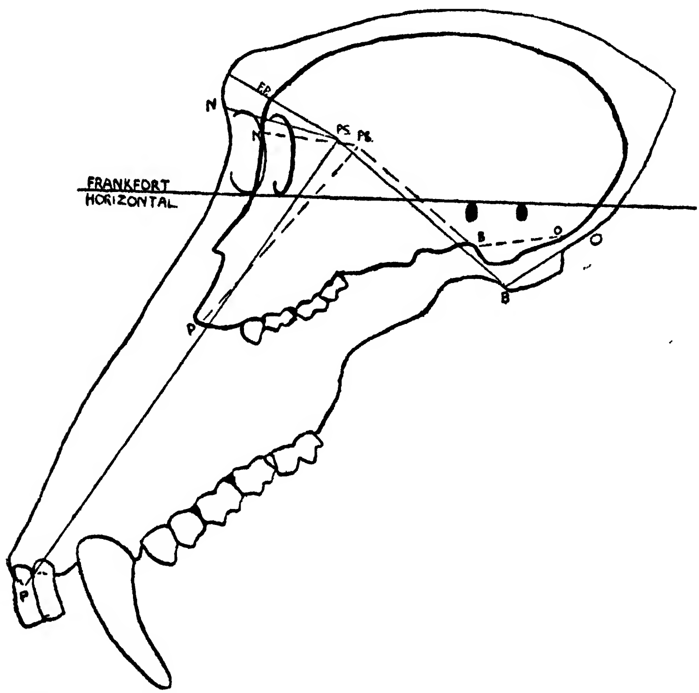
It is clear from the above that in the Baboon the spheno-maxillary angle does not increase in size, but rather decreases (see text-figs. 3 and 4) as the skull ages and becomes more prognathous, a fact which is at variance with the generally-accepted beliefs, not only in regard to the Baboon skull, but in regard to any series of skulls.

These peculiar changes in the spheno-maxillary angle during growth are probably due to the poise of the head. Duckworth, quoting Huxley, writes as follows :—"The so-called facial angle, in fact, does not simply express the development of the jaws in relation to the face, but is the product of two factors, a facial and a cranial which vary independently. The face remaining the same, prognathism may be indefinitely increased or diminished, by the rotation of the frontal end of the skull backwards or forwards upon the anterior end of the basi-cranial axis." This statement may be extended, for the reverse follows as well: viz., the cranial portion remaining the same, the angle varies according to the rotation of the facial. This is what actually happens in the Baboon. The facial part grows definitely downwards and "not almost purely forward," as Huxley put it. Or, in other words, a rotation of the facial axis on the basi-cranial occurs in a downward direction.

Professor Drennan has suggested that the term "subgnathism" should be applied to this downward displacement of the prosthion, and the term "prognathism" should be reserved for the forward displacement. This would analyse the growth of the face into downward and forward components.

The downward growth of the face can be well seen in text-fig. 6, where skulls B. 3 and B. 17 (milk dentition and adult

Text-figure 6.




**Milk dentition skull (B. 3) and Adult male (B. 17) on the Frankfort plane. The basicranial axes and spheno-maxillary angles are figured.**

**P.S.=Prosphenion; N=Nasion; F.P.="Frontal Point"; B=Basion; O=Opisthion; P=Prosthion.**

male stages respectively) are oriented on the Frankfort Horizontal. The angles in relation to the basi-cranial axis are all indicated. the points having been accurately placed by means of the sagittal sections. Whatever objections to the Frankfort Horizontal there may be when applied to the skull as a whole (Keith, 1910, 1925), in respect of the rotation of the facial part of the skulls it affords a valuable method of orientation. The poise of the Baboon skull on this plane, too, is virtually the same as the poise

of the head in the living animal, where the long axis of the skull is definitely directed forwards and downwards, when the animal is in motion, similar to the condition met with in most quadrupeds.

Besides this downward growth or rotation of the prosphenion-prosthion line—as opposed to the forward growth assumed by Huxley and Gregory—another factor also assists in decreasing the size of the spheno-maxillary angle during growth. This factor is the growth which occurs in the middle base of the basi-cranial axis, by which means the prosphenion is pushed forward relative, not only to the basion, but relative also to the facial part of the skull. This second factor can be shown by the length of the middle base—the prosphenion-basion distance—given in Table II. at the various growth-stages. For, in the process of "correction," already mentioned, the face is pushed forward relative to the condyles. Therefore, taking the basion as a relatively fixed point, the varying distance of the prosphenion from it represents the growth which occurs in the middle base.

Briefly summarised, the following points are to be noted, therefore, in connection with the spheno-maxillary angle in the Baboon:—

(1) The spheno-maxillary angle has no value as a criterion of prognathism. It does indicate the degree of downward rotation of the face on the basi-cranial axis ("subgnathism").

(2) This angle does not increase, but, if anything, decreases in size during growth and with the increase in prognathism.

(c) *Alveolar Index.*

With the alveolar index—Flower's Gnathic index—the results as a test of prognathism are more satisfactory. In B. 1 at birth the index is 113. During milk dentition it is 116. In B 7, a stage in the eruption of the permanent teeth in males, just before the appearance of the canines, it is 144. In B. 8, a female without third molars, it is 144. In the adult female it is 155·7 and in the adult male 171.

The figures given by Duckworth for this index are as follows:—

Gorilla, 139·7.
Orang, 155·3.
Chimpanzee, 128·8.
Natives of Australia, 98–108.

This index, then, gives a very fair idea of the actual growth in prognathism in the Baboon skull, and emphasises the fact that the Baboon is more prognathous than any of the Simiidæ. It also demonstrates the fact that the adult male is more prognathous than the adult female skull, which in turn is more so than the skull of milk dentition; and it definitely shows that the skull at birth is least prognathous.

The alveolar index, however, does not take any cognisance of the size of the spheno-maxillary angle, or the amount of inclination

of the facial axis to the basi-cranial. The results of these two criteria—viz., spheno-maxillary angle and alveolar index taken together—emphasises the fact that a downward rotation of the facial axis upon the basi-cranial axis occurs in the Baboon skull with the increase of prognathism which accompanies increasing age.

The values of these two criteria in the case of such skulls as B. 3 (milk dentition) and B. 17 (adult male) placed side by side afford an interesting contrast.

| | Spheno-maxillary angle. | Alveolar index. |
|---|---|---|
| B. 3 .............. | 96° | 115 |
| B. 17 .. ............ | 83° | 172 |

(d) *Facial Triangles.*

The value of the alveolar index as a criterion of prognathism is lessened, owing to the fact that it does not take into consideration the true shape of the facial triangle—the triangle enclosed by the basion-nasion, nasion-prosthion, and basion-prosthion lines. If a proper conception of the growth of the face and the increase in prognathism is to be aimed at, then the values of these dimensions must be considered in relation to one another. This can be effected by expressing the nasion-prosthion and prosthion-basion as percentages of the nasion-basion diameter, as in the following table:—

Table III.

| | Prosthion-nasion. | | Nasion-basion. | | Basion-prosthion. |
|---|---|---|---|---|---|
| At birth (1) .................. | 68·8 | : | 100 | : | 113 |
| Milk dentition (average of 2). | 84·3 | : | 100 | : | 116 |
| Adult female (average of 5). | 127 | : | 100 | : | 156 |
| Adult male (average of 13). | 150·5 | : | 100 | : | 171 |

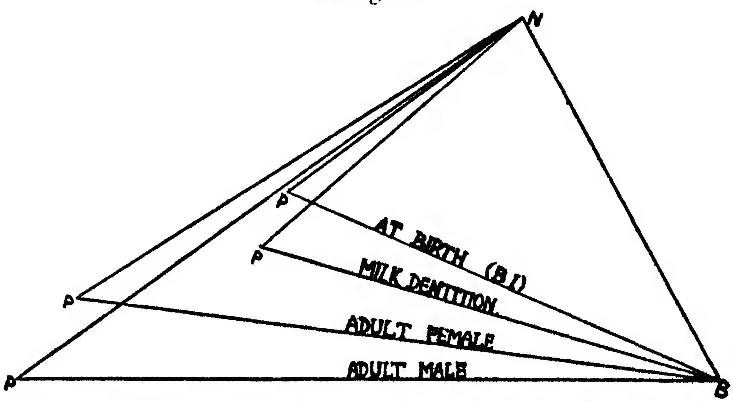
Diagrammatically also, their relationships to one another can be demonstrated as in text-fig. 7, where the facial triangles at various stages of growth are superimposed on a common nasion-basion line. In preparing Table III. and text-fig. 7 the data from skull B. 1 alone were used for the "At birth" stage. Data from skulls B. 2 and B. 3 were used for the milk dentition stage, and the data from five adult female skulls and thirteen adult males in Table I. for the adult female and adult male stages respectively.

Analysing text-fig. 7 according to Professor Drennan's suggestions on the interpretation of prognathism, it is seen that a gradual increase in "prognathism" occurs in the four stages, as evidenced by the forward increase of the line BP. The skull at birth and the adult female are revealed as being less

"subgnathous" than the skulls of milk dentition and adult male respectively.

Summarising the question of prognathism, we find that the study of this problem in the Baboon demonstrates how difficult it is to express it by means of any single index or angle. The spheno-maxillary angle has been shown to be a worthless criterion of prognathism. It merely indicates the rotation of the facial axis on the basi-cranial axis. The alveolar

Text-figure 7.




Facial triangles at different stages of growth superimposed on a common nasion-basion line.

N=Nasion; B=Basion; P=Prosthion.

index, in spite of the fact that it expresses the true degree of prognathism at the various stages of growth of the Baboon skull, nevertheless has the shortcoming that it fails to take into consideration the inclination of the facial axis to the basi-cranial axis. Finally, an attempt has been made to demonstrate the true nature of prognathism in the Baboon skull at various growth-stages by means of the facial triangle.

(3) *Growth of Muzzle and Palate.*

With the eruption of the permanent teeth, especially of the canines, the muzzle, as indicated above in connection with the question of prognathism, elongates considerably.

The following columns in Table I. demonstrate this growth:— Inion-prosthion (1), basion-prosthion (10), nasion-prosthion (12), and nasion-menton (11) lengths, and the orbito-alveolar height (18). The alveolar index, too, is a measure of the elongation of the snout, as are also the proportions of face to cranium at different stages of growth given previously.

With respect to the orbito-alveolar height, it may be mentioned that in young skulls the alveolar border lies perpendicularly

below the orbit and extends posteriorly under cover of the zygomatic arch. As the skull ages and becomes more prognathous, the alveolar border is pushed far forwards, particularly the part bearing the teeth, until it lies well in front of the plane of the orbit. (See Plate I. and text-fig. 1.)

(4) *Nasal Height.*

In young skulls the floor of the nasal fossa extends downwards almost to the prosthion. As the skull ages, the level of the floor rises, until in adult skulls it is situated fully 10 mm. above the level of the prosthion. The nasal bones are fused to each other, either before or immediately after birth. In skull B. 1 they are fused.

(5) *Palatal Area.*

This area was calculated from projected drawings on to squared millimetre paper of the area enclosed laterally by the outer borders of the teeth and more posteriorly by the "tuberosities of the maxillæ," and extending backwards as far as the posterior borders of the horizontal plates of the palatines (as in text-fig. 1) (Keith, 1899).

For the various stages of growth the areas are as follows:—

At birth (B. 1), 7·3 cm.$^2$
Milk dentition (B. 2), 15·3 cm.$^2$
Early stage in eruption of permanent teeth (B. 4), 20·2 cm.$^2$
Canines just erupting (B. 7), 30 cm.$^2$
Stage when third molars are missing (B. 8), 29 cm.$^2$
Adult female, 32·8 cm.$^2$
Adult male, 53 cm.$^2$

(6) *Alveolar Dimensions.*

At birth (B. 1) the upper alveolar breadth is equal to the length (28 mm.–28 mm.). During milk dentition the length is some 5 mm. more than the breadth (39 mm.–45 mm.). In the adult female the breadth is 60 per cent. of the length (average values are: breadth 48 mm., length 79·5 mm.). In the adult male the breadth is 54 per cent. of the length (breadth 55 mm., length 102 mm.).

The palatal proportions are somewhat different.

TABLE IV.

| | Breadth. | Length. | Palato-maxillary index. |
|---|---|---|---|
| At birth (B. 1) | 16 mm. | 23 mm. | 69·6 |
| During milk dentition (average of two) | 21 mm. | 39 mm. | 54 |
| Adult female (average of five) | 25·6 mm. | 70·6 mm. | 36·25 |
| Adult male (average of thirteen) | 30·6 mm. | 95·4 mm. | 32 |

### (*d*) Endocranial Cavity.

From a study of the cranium and endocranial casts a knowledge of brain-growth may be derived. On this account, therefore, possibly no part of the skull is more deserving of notice in the study of growth than the brain-box.

It has been found necessary to introduce the question of Baboon brain-growth by a brief note on anthropoid brain-growth. In the first place most of the work in this field has been done on the anthropoids, and in the second, the growth-changes which occur in the Baboon brain-box are in the main of the same nature and due to the same causes as in the higher anthropoids.

The main conclusions on anthropoid brain-growth may be summarised as follows:—

Keith (1910) writes as follows:—"The age-changes in the anthropoid skull have little or nothing to do with the brain-growth, for by the end of the first year, if not earlier, their brains cease to grow." Virchow (quoted by Macnamara, 1902) states that the Ape's brain reaches perfection before the shedding of the teeth, and ceases to grow at this stage. Duckworth (1915) similarly writes "That nothing is more impressive in the Gorilla than the small amount of brain-growth after infancy." Topinard, (1867), however, records an increase of 22 per cent of the cranial capacity in the Orang between the period of the eruption of the permanent teeth and maturity.

Keith (1910) further states that the cranial capacity in large anthropoids actually decreases with age, and the decrease affects the vertical diameter of the skull, measured from the upper surface of the presphenoid to the internal bregma. This statement is qualified by Duckworth (1915), who writes that "even if actual diminution of the vaulting is demonstrable, the arrest or diminution is not absolute . . . ., and compensation takes place by way of an increase in transverse width."

A more detailed consideration of the growth of the anthropoid brain is beyond the scope of this paper, but observations which I have made on four skulls of young Chimpanzees and Gorillas seem to indicate that there cannot be, as Keith maintains, an abrupt cessation of brain-growth on the attainment of a complete milk dentition.

These young anthropoid skulls are all at stages during or just subsequent to the period of milk dentition. Three have cranial capacities, measured from endocranial casts, well below the lowest value recorded in the adult female of their group. This indicates that a certain amount of brain-growth must occur after the stage of milk dentition in the anthropoids. The Baboon skull certainly shows that brain-growth takes place after the period of the deciduous dentition.

It appears, therefore, in view of the above evidence and of my findings in the Baboon, that the question of anthropoid brain-growth requires re-investigation.

*Growth of Endocranial cavity in the Baboon.*

In addition to the usual cranial dimensions in Table I. and the cranial capacity of each skull measured by shot, endocranial casts were made, for the purpose of this study, of the skulls enumerated in the table below. The brains of skulls B. 1, B. 8. and B. 17, which had been in formalin for some months, were also available. Details of the casts and brains are given in the following tables:—

TABLE V.

| | B. 1. | B. 3. | B. 4. | B. 7. | B. 8. | B. 10. | B. 11. | B. 13. | B. 14. | B. 17 |
|---|---|---|---|---|---|---|---|---|---|---|
| Cranial capacity by shot. | — | 165 | 175 | 182 | 163 | 170 | 175 | 187 | 203 | 225 |
| Volume of endocranial casts. | 108 | 183 | 180 | 191 | 173 | 183 | 192 | 200 | 210 | 240 |
| Max. ant. post. diam. of casts. | 75 | 95 | 94 | 93 | 90 | 90 | 91·5 | 97 | 96 | 100 |
| Max. trans. diam ... | 59 | 74 | 76 | 74 | 73 | 73·5 | 75·5 | 74·5 | 78 | 79·5 |
| Height of cerebrum above subcer plane | 34 | 36·5 | 37 | 35·5 | 35·5 | 36 | 38 | — | 36·5 | 38 |
| Basion int. bregma diameter. | 47 | 58 | 60 | 65 | 61 | 64 | 64 | 66 | 67 | 72·5 |
| Height of casts from lower surface of temporal lobes. | 46 | 55·5 | 56·5 | 59 | 55 | 58 | 60 | 57 | 58 | 63 |

TABLE VI.—Brains.

| | Volume. | Weight. |
|---|---|---|
| B. 1 ... .. . | 78 c.c. | 73 grams. |
| B. 8 . . .. . | 110 c.c. | 118 ,, |
| B. 17 ...... ......... | 186 c.c. | 189 ,, |

It will be noticed that in each case the cranial capacity as measured by shot is less than the volume of the endocranial cast of the same skull, the average difference being 13 c.c. It is probable that the volume by shot is slightly too little and the volumes by the casts are slightly too large. A mean between the two will give the skull capacity fairly accurately, and to bring the cranial capacities of those skulls in Table I., estimated only by shot, into line with the others, 6·5 c.c. has been added to each. The relative values of the capacities are not thereby altered.

The data denote a definite increase in cranial capacity, and therefore in the size of the brain, after milk dentition, especially in the case of male skulls.

Soon after birth (B. 1) the cranial capacity is 108 c.c. During milk dentition, 170 c.c. (average of B. 2 and B. 3), an increase of

57 per cent. During the period of eruption of the permanent teeth in the female (B. 6 and B. 8) the capacity is 170·5 c.c. In the adult female the capacity is 176·9 c.c. (average of five), an increase of but 4 per cent. in terms of the capacity during milk dentition. The same two stages in the male skulls show the following capacities:—184·5 c.c. (B. 4 and B 7), an increase of 8·5 per cent. relative to the capacity during milk dentition, and 208 c.c. (average of thirteen), an increase of 22 per cent. in the period between the shedding of the milk teeth and complete permanent dentition. The increase from the stage in the eruption of the teeth represented by B. 4 and B. 7 to the mature condition is 12·7 per cent.

It may be noted in passing that Hrdlicka (1925) gives the range of capacity in the Baboon as 120–200 c.c. in the male, and 120–160 c.c. in the female. The range as I find it is 191·5–232·5 c.c. in the *adult* male, and 171·5–181·5 in the *adult* female.

The cranial capacity in the adult female is 15 per cent. less than that of the adult male. Duckworth (1915), quoting Oppenheim, gives the ratio between the capacities of male and female *Cynocephalus* as 100 : 83.

In the face of these facts, it is impossible to deny a definite increase in the size of the brain during the period of eruption of the permanent teeth, a time before which the anthropoid brain is generally supposed to have attained its maximum size. The fact that the female brain undergoes an increase in size after milk dentition relatively small as compared with that of the male is not surprising when one considers the general physical superiority of the male.

I have tried to discover in which dimensions the brain increases in size after milk dentition.

### *Height of the Brain.*

It was found that the increase in capacity is not due to any increase in height of the cerebrum; in this respect the Baboon is similar to the Gorilla and other anthropoids. Growth of the cerebrum causes expansion of the parietals, and in the Baboon the increase in the size of the parietals is very limited, being barely 1 cm. in any direction during the whole process of growth. After milk dentition they do not increase in height, though the length may be increased slightly.

The absence of any increase in height above the subcerebral plane can be shown by means of the following measurements:—

(a) *Auriculo-bregmatic Height.*—The value of this criterion is lessened owing to the greater thickness of bone and to the growth of crests in older skulls. Average dimensions are:—

At birth (B. 1), 45 mm.

During milk dentition, 52·5 mm.

Adult female, 52·6 mm.

Adult male, 56 mm. (The large size of this measure- is chiefly due to the thickness of bone in the region of the bregma.)

(b) *The Height of the Vault above the Subcerebral Plane.*—This dimension can be taken only on skulls sagittally sectioned in the median plane. When oriented in this plane, the presphenoid is situated well in front of the internal bregma, and it was found necessary to connect the level of the floor of the anterior cranial fossa with the transverse sinus posteriorly by means of tape, and to measure the greatest perpendicular height from the tape to the vault. (In most cases it was found that the internal bregma is not quite the highest point of the vault, this point being found more posteriorly.)

At birth (B. 1) this height equals 34 mm.
During milk dentition (B. 3), 36·5 mm.
Adult female (B. 10 and B. 11), 37 mm.
Adult male (B. 14 and B. 17), 37·5 mm.

It should be noted that no diminution in the vaulting occurs.

After the shedding of the deciduous teeth, the brain continues to grow in the regions below the subcerebral plane, *i. e.* in the temporal lobes and the cerebellum. The effect of this growth is to expand the brain-box in these regions. That such expansion does occur can be seen from the height of the squamous temporal bone during milk dentition and in adults. In older skulls this bone is definitely higher. The fact that there is growth in the cerebellum and temporal lobes is shown by the following measurements:—

(a) *Basion-external bregma Height*:—

At birth (B. 1), 48·5 mm.
During milk dentition (av. of B. 2 and B. 3), 60 mm.
Adult female (av. of five), 67 mm.
Adult male (av. of thirteen), 74 mm.

(b) *Basion-internal bregma Height.*—These measurements are taken from the casts in Table V.:—

At birth (B. 1), 47 mm.
During milk dentition, 57 mm.
Adult female, 64 mm.
Adult male, 68 mm.

Observations on the thickness of the bone in the region of the bregma in the skulls sectioned give the following values:—

At birth (B. 1), 1·5 mm.
During milk dentition, 2 mm.
Adult female, 3 mm.
Adult male, 4 mm.

(c) *Distance from the lower surface of the temporal lobes to the highest point on the casts* (Table V.):—

At birth (B. 1), 46 mm.
During milk dentition, 55·5 mm.
Adult female, 59 mm.
Adult male, 60 mm.

As has been shown, there is no increase in height above the subcerebral plane after the shedding of the deciduous teeth, and, as there is a definite increase in the basion-bregma diameter after this period, the only conclusion that can be arrived at is the one given above, viz. that growth of the brain occurs in the cerebellum and temporal lobes.

*Length of the Brain.*—Reference to Table I. shows a gradual increase in the maximum antero-posterior diameter of the cranium as the skull ages.

At birth (B. 1) it is 78·5 mm.
During milk dentition it is 99 mm.
In the adult female it is 109 mm.
In the adult male it is 118 mm.

Table V. gives the maximum antero-posterior diameters of a group of endocranial casts, but these dimensions do not show any regular increase as do the maximum antero-posterior diameters of the cranium. At birth (B. 1) the length of the endocranial cast is 75 mm. During milk dentition it is 95 mm. In the adult female it is 90 mm., and in the adult male 97·5 mm.

A very slight increase in length occurs in the group of male skulls, after the shedding of the milk teeth. The series does not indicate what the condition is in the female as regards the growth in length. It may be mentioned, however, that the adult female brain is 7 mm. shorter than the male.

Seeing, then, that the increase in the length of the brain after the shedding of the deciduous teeth is more or less negligible, the increase in the length of the skull must be due to increased thickness of the bone in the glabella and inion regions.

*Transverse diameter of the Brain.*—Increase in this diameter after the period of milk dentition is more marked than in the antero-posterior. The following measurements are taken from Table V.:—

Width at birth (B. 1), 59 mm.
During milk dentition, 74 mm.
Adult female, 74·25 mm.
Adult male, 77 mm.

Again, as in the former dimension, the increase is more marked in the male. Reference to the maximum transverse diameter of the skull in Table I. also demonstrates this growth in width after the shedding of the milk teeth. The changes in the thickness of the bone are more or less the same in the region in which the measurements were taken, as in the region of the bregma.

At birth the maximum transverse diameter is 61·5 mm.
During milk dentition, 75 mm.
Adult female, 77·8 mm.
Adult male, 83·4 mm.

A series of the normæ verticales of the various endocranial casts projected on to millimetre paper showed a slight progressive increase in area up to the adult condition, more especially in the transverse direction.

*Summary of the Growth of the Endocranial Cavity.*—It was found, from the skulls studied, that the endocranial cavity of the adult male Baboon was 22 per cent., and that of the adult female 4 per cent. larger than the endocranial cavity of the Baboon during milk dentition. These facts indicate a growth in the Baboon brain after the period of the shedding of the deciduous teeth, a process which Keith states does not occur in the anthropoids.

On analysis it was found that the growth which took place during this period occurred chiefly in the cerebellum and temporal lobes, for the height of the endocranial cavity above the subcerebral plane did not increase during the period, whereas the basi-bregmatic height did. During the period subsequent to the milk dentition the increase in length and breadth is very slight.

## (5) Summary.

(1) The prosthion-inion length, the transverse diameter, and the basi-bregmatic height continue to increase from birth until a time considerably subsequent to the eruption of the permanent teeth.

(2) The varying proportions of face to cranium at the different stages of growth are demonstrated in the text and diagrams.

(3) Virtually all the cranial sutures of the Baboon skull, unlike those of the higher anthropoids, are never completely occluded, even in the aged male.

(4) The basicranial axis and its angles are of a type which finds its closest counterpart in those of the anthropoids.

(5) The spheno-maxillary angle in the Baboon has an average value of 90° 30′, and is therefore well within the human range. This angle, far from being "the most important angular measurement by which prognathism can be represented" (Duckworth), is *worthless* as a criterion of prognathism. It does, however, indicate the degree of "subgnathism."

(6) The spheno-maxillary angle in the Baboon does *not* increase with the eruption of the permanent teeth and with the growth of the muzzle. This lack of increase during growth is explained by a downward rotation of the muzzle upon the basi-cranial axis.

(7) Flower's gnathic index is shown to be a reasonable criterion of the degree of prognathism in the Baboon skull.

(8) Prognathism in the Baboon has been studied by means of the facial triangle (text-fig. 7 and Table III.), which, in my opinion, expresses most clearly its nature and degree.

(9) The growth-changes in the cephalic index, temporal lines temporal fossæ, nuchal area, occipital plane, base of skull, and palatal and alveolar dimensions are of a nature comparable with the growth-changes in the higher anthropoids.

(10) An increase of 22 per cent. occurs in the volume of the endocranial cavity in the male Baboon, and 4 per cent. in the female, between the period of milk dentition and maturity.

(11) This later brain-growth takes place chiefly in the temporal lobes and cerebellum, and very slightly in the length and breadth of the cerebrum. No growth at all takes place in the height of the cerebrum above the subcerebral plane after the period of the milk dentition.

In conclusion I wish to express my indebtedness to Professor M. R. Drennan for his kindly advice and criticism during the progress of the investigation, and to Professor Raymond A. Dart, of the University of the Witwatersrand, for reading a draft of the paper and for valuable advice.

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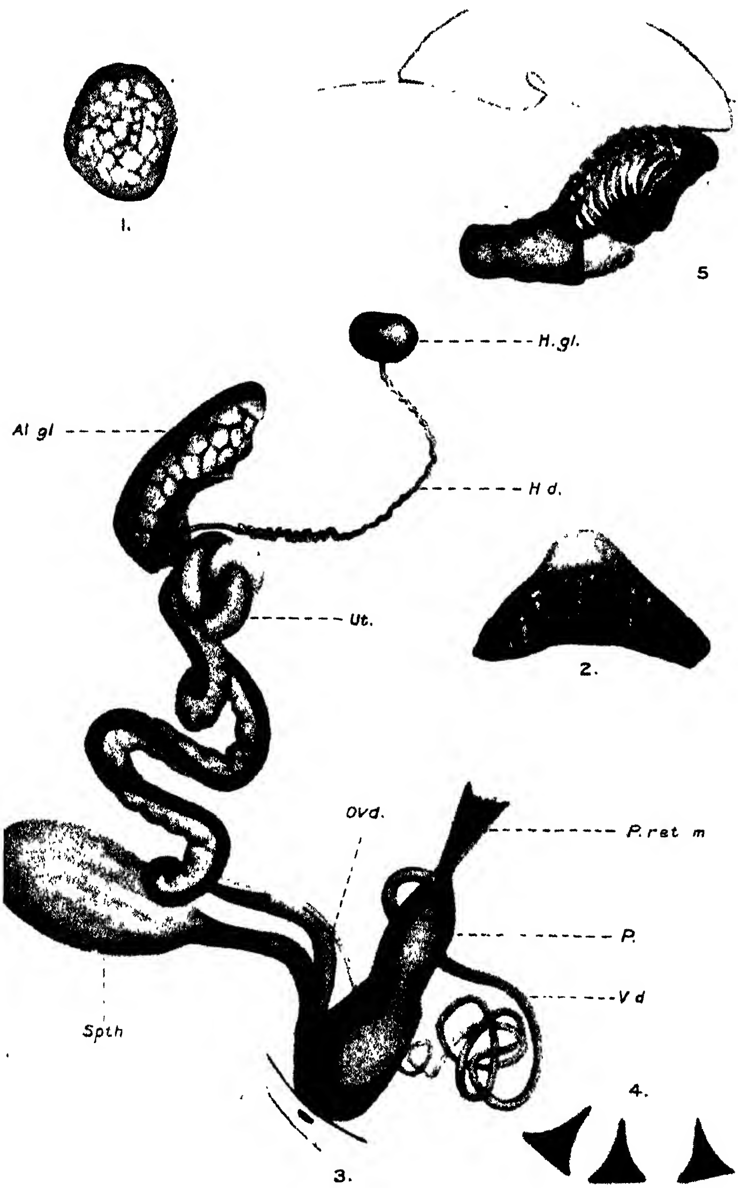
## EXPLANATION OF THE PLATE.

Complete Skulls from left to right: Adult male Z. 2. Adult female Z. 1. Skull of Milk Dentition B. 2. Skull at Birth B. 1.

Sagittal sections of Skulls from left to right: Skull of Milk Dentition B. 3. Male: B. 4. Stage in eruption of permanent teeth: Adult female B. 11: Adult male B. 17. The basicranial axis and spheno-maxillary angle are indicated in each section.

Sagittal sections of skulls from left to right: Skull of Milk Dentition B. 3. Male: B. 4. Stage in eruption of permanent teeth: Adult female B. 11 Adult male B. 17.

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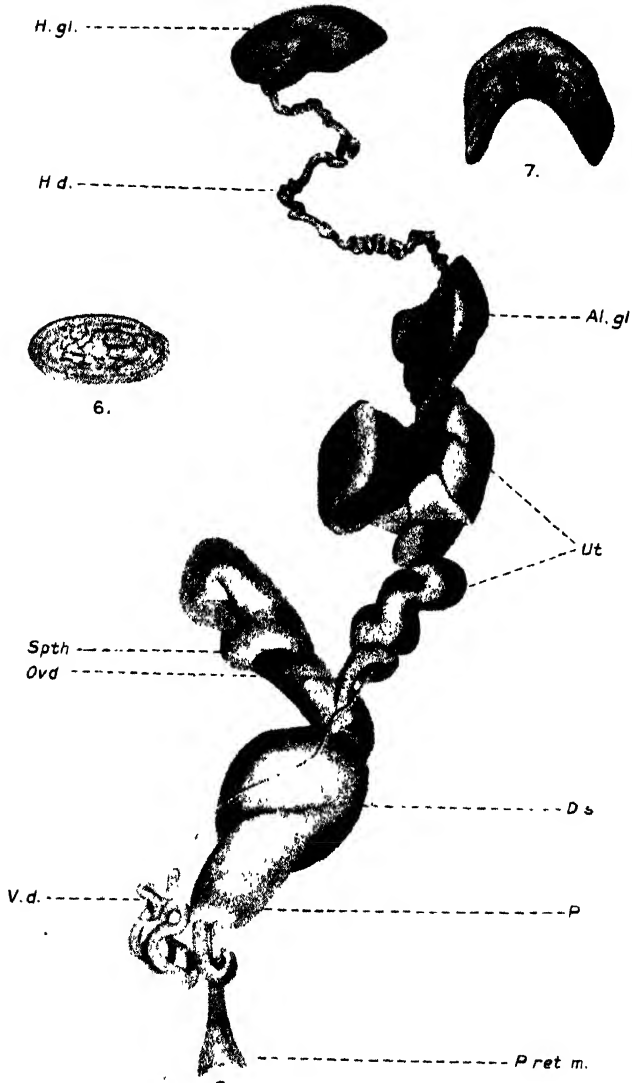
NEW SPECIES OF *Anadenus* (MOLLUSCA).

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NEW SPECIES OF *Anadenus* (MOLLUSCA).

# 43. On Three New Species of the Genus *Anadenus* (Mollusca). By D. Bhatia, M.Sc., F.R.M.S. (Zoology Laboratory, Cambridge) *.

[Received May 14, 1926: Read June 15, 1926.]

(Plates I. & II.†; Text-figures 1–4.)

An account is given in this paper of three new species of the Slug *Anadenus* occurring in India, at Dalhousie (Punjab), Lahore (Punjab), and Gulmarg (Kashmir) respectively. The specimens of these species were collected mainly with a view to study the cytology of the hermaphrodite gland. The species from Gulmarg, for reasons given below, has been placed in a subgenus, *Gymnanadenus*, as suggested by the late Dr. Annandale.

The specimens were studied in the Zoological Laboratory of the Government College, Lahore, and the laboratories of the Zoological Survey of India, Calcutta.

My grateful thanks are due to Professor George Matthai for allowing me to work through his collection. I must also thank the late Dr. N. Annandale, C.I.E., F.R.S., Director of the Zoological Survey of India, for his useful criticism and suggestions.

## Family ARIONIDÆ.

### Subfamily Arioninæ.

### Genus Anadenus Heynemann.

1863. Heynemann, Malakol. Blätter, Bd. x. p. 138.
1882. Godwin-Austen, Moll. Ind. vol. i. p. 46.
1893. Cockerell, 'The Conchologist,' vol. ii. p. 192.
1898. Pilsbry, Proc. Malac. Soc. vol. iii. p. 94.
1914. Gude, The Fauna of British India, Mollusca, vol. ii. p. 468.

The body is convex and is without a keel; the posterior extremity is bluntly pointed. The two upper tentacles are longer than the lower ones. The trunk is fused with the foot along its entire length. The respiratory orifice is on the right side of the mantle, towards the posterior end. The foot is tripartite and the pedal gland is absent. An internal shell is present, which may be complete or fragmentary. The jaw is closely ribbed. The tooth-plates of the radula are rectangular,

* Communicated by the Secretary.
† For explanation of the Plates see page 884.

with projecting sides. The central tooth is symmetrical, somewhat triangular in shape, and bears a pair of lateral denticles. The lateral teeth are similar in shape to the central, each with a denticle on the outer side only. The outermost lateral teeth usually possess one or two accessory denticles.

### ANADENUS DALHOUSIENSIS, sp. n.

Specimens when fully extended vary from 145 mm. to 200 mm. in length and 30 mm. to 40 mm. in breadth. The trunk decreases in width towards the posterior end. The line of fusion with the foot has a frilled appearance. Rhomboidal areas occurring on the dorso-lateral surface of the body, are about 4 mm. in length, and are separated from one another by very shallow grooves. The mantle is fused with the trunk except at the anterior margin, which remains free in the form of a flap. The length of the mantle as compared with the trunk (excepting the head-region) is in the ratio of 1 : 2. The median region of the mantle-wall is granular in appearance, while the lateral regions are irregularly grooved. On contraction these grooves become indistinct*. The genital aperture lies a little behind the right eye-tentacle. The foot is bluntly pointed at its posterior extremity and presents a concavity at the anterior end. The grooves on the lateral regions of the foot are more pronounced than those on the central region.

The colour is somewhat variable. Most of the specimens were pale brown with reddish-brown streaks, while some were orange-brown with red streaks and black spots. The head is black above but lighter below and at the sides. The central area of the foot is pale brown, while the lateral areas are of a darker shade.

The shell (Pl. I. fig. 1), which is covered by the mantle, is 18 mm. long and 15 mm. broad. It is composed of a thin conchiolin base, to whose lower surface irregular calcareous pieces are attached, the margin of the conchiolin base being distinct.

The jaw or mandible (Pl. I. fig. 2) is crescentic in shape and red in colour, and forms a dorsal arch at the anterior end of the buccal cavity. It is produced behind into a thin, colourless, chitinous plate, and bears 12 to 14 somewhat curved ribs on its anterior surface. The usual number of these ribs is 13.

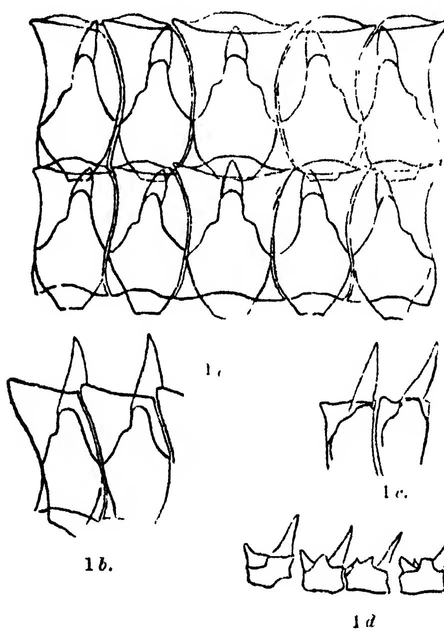
The radula (text-figs. 1 *a*, 1 *b*, 1 *c*, 1 *d*) consists of curved rectangular plates arranged in parallel rows. Each plate bears a tooth which is broad proximally and conical distally. The teeth constitute 155 longitudinal and 160 transverse rows. Those forming the median longitudinal row are broader than the others. The mesocones are sharp but the ectocones blunt. The distal portions of the lateral teeth become gradually elongated from the median row outwards, but are slightly bent inwards.

* The descriptions of *Anadenus* given by Heynemann and Pilsbry appear to be based on preserved specimens.

The marginal teeth are small, with distinct mesocones and ectocones. Small accessory denticles arise from the bases of some of the marginal teeth.

The kidney, which is a horseshoe-shaped organ lying in the posterior region of the mantle-cavity, surrounds the pericardium. It is spongy in texture, and its dorsal surface is covered by pulmonary veins. A thin-walled ureter, the aperture of which is situated in the pulmonary orifice, arises from its right side.

Text-figure 1.




*Anadenus dalhousiensis*, sp. n.

1 *a*. Central and proximal lateral teeth of radula.
1 *b*, 1 *c*. Lateral teeth of radula.
1 *d*. Peripheral teeth of radula.

The heart lies in the pericardium and consists of an auricle and a ventricle. The auriculo-ventricular aperture, which is excentric in position, is slit-like and provided with a sphincter, but without a valve. The auricle is thin-walled, and receives in front a number of pulmonary veins communicating with the rich vascular network in the roof of the mantle-cavity. The ventricle, which is thick-walled and conical, lies behind the auricle and is partially covered by the latter. A short aorta

arises from the hind end of the ventricle, and immediately divides into a *cephalic aorta* running forwards to supply the reproductive organs, anterior part of the alimentary canal, salivary glands and head, and a *hepatic aorta* which runs backwards to supply the intestine and the liver.

The nervous system is of an advanced Hypoathroid type, inasmuch as the principal pairs of ganglia have undergone complete fusion. The pleural and visceral ganglia form a common pleuro-visceral mass lying below the œsophagus and just above the pedal ganglia. Pleuro-pedal connectives are consequently very short, while the cerebro-pedal and cerebro-pleural connectives run backwards on each side of the œsophagus. Buccal ganglia lie below the œsophagus near its proximal end, and are connected with the cerebrals by buccal nerves and with each other by means of a commissure.

The hermaphrodite gland (Pl. I. figs. 3, 4, 5) is situated behind the stomach between the right and left lobes of the liver. The hermaphrodite duct runs forwards, being thrown into zigzag coils, but becoming straightened out towards the distal end. It opens into a transverse ductule which is blind at one end but communicates by the opposite end with the uterus. The albumen gland, which is large and yellowish, opens into the uterus at the junction of the latter with the hermaphrodite duct. The uterus is a thin-walled coiled tube. Proximally the coils of the uterus form a large mass; the distal portion, though not coiled, is thrown into puckered folds. Part of the uterus wall from its commencement is slightly constricted off along its entire length to form a yellow band. The constriction becomes complete towards the anterior end of the uterus. The yellow band forms a separate duct—the vas deferens, while the continuation of the uterus becomes the oviduct. The oviduct is smooth-walled and opens into the genital cloaca. Communicating with the distal end of the oviduct is a thick-walled spermathecal tube lying on the right side of the oviduct and becoming continuous behind with a thin-walled sac—the spermatheca. The vas deferens, which is a very narrow tube, runs along the left side of the oviduct, and becomes somewhat wider as it passes forwards below the penis. In front of the penis it becomes highly convoluted, the mass of coils lying just behind the left eye-tentacle. The terminal portion of the vas deferens, as it emerges from the mass of coils, turns backwards and opens into the posterior extremity of the penis. The penis is a thick muscular sac attached to the posterior margin of the mantle-cavity by means of a retractor muscle which arises close to the opening of the vas deferens. The inner surface of the wall of the penis is raised into numerous chitinous processes triangular in shape. The anterior end of the penis opens into a wide muscular dart-sac which communicates with the genital cloaca. The dart-sac contains calcareous tooth-like processes or darts which arise from small, curved, calcareous rods embedded in its muscular

wall, five or six teeth arising from the same rod. At the opening of the penis into the dart-sac is a flat calcareous plate from which 12 toothless calcareous rods arise. The calcareous plate and teeth are frequently exposed by the eversion of the dart-sac.

There is a considerable resemblance, in respect of size and colour, between this species and *Anadenus altivagus*, as described by Theobald (Cat. Land and Freshwater Shells Brit. India, 1876, Addenda, p. i, and Journ. of Asiatic Soc. Bengal, vol. l. 1881, p. 47), and subsequently by Godwin-Austen (Moll. Ind. vol. i. 1882, p. 49), by Cockerell ('The Conchologist,' vol. ii. 1893, p. 192), and by Pilsbry (Proc. Malac. Soc. London, vol. iii. 1898, p. 95).

The descriptions of *A. altivagus* given by Godwin-Austen and Pilsbry differ slightly in regard to the retractor muscles and the genitalia. Godwin-Austen figures (plate vii. fig. 5) the retractor muscle of the penis attached to the mantle on the right of the pharyngeal retractor. *A. dalhousiensis*, however, agrees with Pilsbry's description, for the retractor muscle of the penis is attached to the left of the pharyngeal retractor.

In the genitalia the chief differences between the two accounts are in the shape of the penis, size of the spermatheca, and the structure of the dart-sac. In all these, *A. dalhousiensis* agrees more with Godwin-Austen's *A. altivagus*.

Another allied species is *A. sechuenensis* from China (Collinge, 1899, Journ. of Malac. vol. vii. p. 78), but it differs from *A. dalhousiensis* in having a bifurcated penis-retractor muscle which is attached to the organ at two places. Besides, the size of the penis and receptaculum seminis is proportionately much smaller.

Apart from the above-mentioned differences, *A. dalhousiensis* differs from *A. altivagus* in the following:—The shell is comparatively thick and consists of calcareous pieces; the jaw has a chitinous plate attached to it; the number of jaw-ribs varies from 12 to 14. The radula has 155 longitudinal rows of teeth (111 in *A. altivagus*), and the calcareous plate in the dart-sac is not perforated.

All the above anatomical details are of specific value.

*Locality.*—Dalhousie (Punjab).

### Anadenus lahorensis, sp. n.

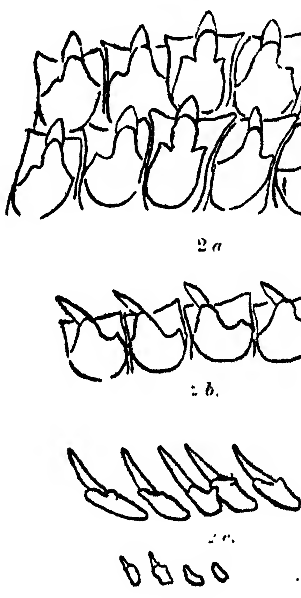
Specimens, when fully extended, measure 20 mm. in length and 4 mm. in breadth. The trunk is marked by regular polygonal areas separated by shallow grooves. The mantle is about 7 mm. in length and has a granular surface. The head is narrower than the body and can be extended for about 4 mm. On the dorsal surface a prominent ridge runs along the median line of the head and extends forwards up to the oral orifice. The genital aperture lies behind the right eye-tentacle. The respiratory and anal apertures are separate. The latter lies just

behind the mantle-slit. The lateral areas of the foot are narrower than the central area and are granular in appearance.

The colour is dark grey. Black pigment, in the form of tiny spots, occurs on the dorsal surface of the trunk, mantle, and head. The sides of the head are quite colourless and the skin is more or less transparent. The two pairs of tentacles are black. The lateral areas of the foot are colourless, while the central area is light grey.

The shell (Pl. II. fig. 6) is oval in shape and is moderately

Text-figure 2.




*Anadenus lahorensis*, sp. n.

2 *a*. Central and proximal lateral teeth of radula.
2 *b*, 2 *c*. Lateral teeth of radula.
2 *d*. Peripheral teeth of radula.

thick and flat. It is 4 mm. long and 2 mm. broad. As in *A. dalhousiensis*, the shell consists of numerous calcareous pieces loosely attached to the lower surface of a chitin-like base.

The jaw (Pl. II. fig. 7) is crescentic in shape and light red in colour. The ribbing on the front surface is faint and irregular, and confined to only the central region. The exact number of ribs could not be made out.

The radula (text-figs. 2 *a*, 2 *b*, 2 *c*, 2 *d*) consists of 111 transverse and 91 longitudinal rows of teeth. The teeth of the

median row are narrow and have their mesocones constricted at their bases. The lateral teeth resemble those of *A. dalhousiensis*, except that the ectocones are more prominent and placed on broader bases, and are well separated from the mesocones. The ectocones get gradually reduced in size towards the outer lateral teeth, and are completely lost in the outermost. The marginal teeth are thus simply aculeate.

The kidney lies towards the posterior region of the mantle-cavity and is produced behind into a big lobe. The ureter opens out through the anal aperture.

The general arrangement of the reproductive system is the same as in *A. altivagus* and *A. dalhousiensis*. The dart-sac is, however, comparatively narrow and devoid of calcareous darts and plate.

The species resembles *A. dalhousiensis* in the nature of the shell and of the radula (in the number of teeth it agrees with *A. altivagus*) and in the general arrangement of the reproductive organs. It differs from *A. dalhousiensis* in regard to size, external features, nature of the dart-sac, and the position of the anal aperture.

It differs from *A. dalhousiensis* in size and external features, and resembles *A. modestus* (Theobald in Nevill, Sci. Res. Second Yarkand Mission, Mollusca, 1878, p. 21; Godwin-Austen, Moll. Ind. i. 1882, p. 53; Cockerell, 'The Conchologist,' ii, 1893, p. 192) in these respects.

The separation of the anal and respiratory apertures is, however, the most characteristic feature of this species, and distinguishes it from all the recorded species of the family Arionidæ.

The only other slug with an identical position of the anal and respiratory apertures is *Hyalimax* (Godwin-Austen, Moll. Ind. i. 1882, p. 55), belonging to the family Succineidæ.

This resemblance, however, does not indicate any affinities between the two forms, although on account of other reasons (shell) the genus *Hyalimax* was at one time described as a subgenus of *Limax* (H. & A. Adams, Genera Rec. Moll. ii. 1855, p. 219). The above is only a case of analogy, perhaps like the analogous seriation of the nature of shell that occurs in both Succineidæ and Arionidæ (Fischer, Journ. Conchyl. xv. 1867, p. 218). *A. lahorensis* differs from *Hyalimax* in most characters, viz. jaw, radular teeth, shell, reproductive organs, etc.

*Locality.*—Botanic Gardens, Lahore (Punjab).

### Subgenus Gymnanadenus, nov.

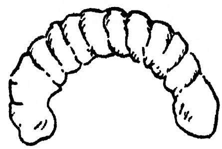
The shell is fragmentary. The outermost lateral teeth of the radula are usually without or with poorly-developed accessory denticles. The penis is as wide as the dart-sac.

### Anadenus matthaii, sp. n.

Specimens in alcohol vary from 90 mm. to 115 mm. in length and 35 mm. to 40 mm. in width. On preserved specimens it is

not possible to determine the pattern of the surface of the body. The mantle is about 35 mm. long, and, as in the preceding species, is granular in the median region and irregularly grooved at the sides. The genital aperture is midway between the right

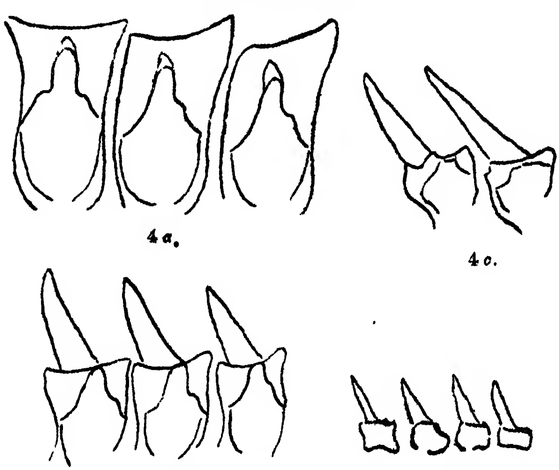
Text-figure 3.



3.
*Anadenus matthaii*, sp. n.
Jaw.

eye-tentacle and the respiratory orifice. The lateral areas of the foot are nearly as wide as the median area in the central region of the foot, but gradually become narrower towards the

Text-figure 4.



4 *a*. 4 *c*. 4 *b*. 4 *d*.

*Anadenus matthaii*, sp. n.

4 *a*. Central and proximal lateral teeth of radula.
4 *b*, 4 *c*. Lateral teeth of radula.
4 *d*. Peripheral teeth of radula.

extremities. The anterior edge of the foot is concave as in *A. dalhousiensis*.

The colour is pale grey. The dorsal surface of the head is somewhat black, the tentacles being of deeper tint. The sides

of the head are more or less white. The median area of the foot is pale brown, while the lateral areas are of darker shade.

The shell is fragmentary, being represented by numerous fine calcareous granules in the median area.

The jaw or mandible (text-fig. 3) is crescentic in shape and dark brown in colour. The sides are without ribs, while 8 or 9 curved ribs are visible in the mantle-wall.

In the radula the teeth are arranged to form 115 longitudinal and 138 transverse rows. The teeth of the median longitudinal row (text-figs. 4 *a*, 4 *b*, 4 *c*, 4 *d*) are comparatively narrow, the mesocones short and the ectocones blunt. The lateral teeth resemble those of *Anadenus dalhousiensis*, the mesocones getting elongated from the median row outwards and slightly bent inwards. The marginal teeth have very minute ectocones, and no accessory denticles.

The kidney is horseshoe-shaped as in *A. dalhousiensis*, and appears to be longer than broad in preserved specimens.

The reproductive system (Pl. II. fig. 8) differs from that of *A. dalhousiensis* in the following respects:—

The hermaphrodite gland is comparatively larger, forming an elongated mass measuring 12 mm. in length. The uterus is more closely coiled. The spermathecal tube is wider but the spermatheca is smaller. The penis is almost as wide as the dart-sac. The dart-sac is without a calcareous plate.

*A. matthaii* agrees more closely with *A. beebei* (Cockerell, Bull. Amer. Mus. Nat. Hist. vol. xxxii, 1913, p. 617) than with any other recorded species. The resemblance is confined to the size, general proportion of parts, and the nature of the jaw. The former, however, differs from the latter in the following respects:—

1. The colour of the preserved specimens is pale grey, and not warm ochreous as in *A. beebei.*
2. The shell is fragmentary, whereas *A. beebei* has a continuous membranous shell containing minute calcareous particles.
3. The outermost rows of radular teeth are without accessory denticles.
4. The penis is as wide as the dart-sac.
5. The dart-sac contains calcareous darts which are said to be absent in *A. beebei.*

In regard to the absence of accessory denticles in the marginal teeth of the radula, *A. matthaii* differs from the genus *Anadenus* as described by Godwin-Austen (Land and Freshwater Mollusca of India, ii, 1882, pp. 49, 50). He remarks:—"The outermost laterals are oblong at the base, with one long blunt tooth and one or two small teeth disunited and separate from it, but rising from the same base (plate vi. figs. 6 *a*, 6 *b*). The outer teeth are very characteristic of the genus, for nothing like them is to be found in either *Arion* or *Limax.*"

The absence of a complete shell is another striking difference from the genus *Anadenus*. *A. matthaii* resembles in this respect

the genus *Arion*, where the shell is fragmentary, as described above.

The presence of a robust penis, nearly as wide as the dart-sac, distinguishes *A. matthaii* from the descriptions and figures given of the recorded species of the genus.

Considering these important points of contrast with the generic characters, it has been thought advisable to put *A. matthaii* in a distinct subgenus, for which the name *Gymnanadenus* is suggested.

*Locality.*—Gulmarg (Kashmir).

### *Explanation of Lettering employed.*

*Al.gl.* Albumen gland. *H.d.* Hermaphrodite duct. *H.gl.* Hermaphrodite gland. *Ovd.* Oviduct. *P.* Penis. *P.ret.m.* Retractor muscle of the penis. *Spth.* Spermatheca. *Ut.* Uterus. *V.d.* Vas deferens.

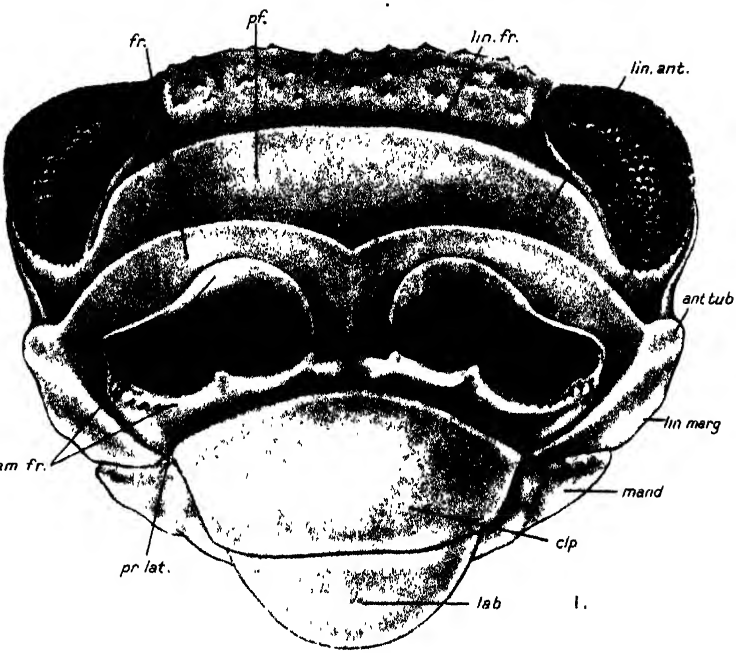
## EXPLANATION OF THE PLATES.

### PLATE I.

Fig. 1. Shell—*Anadenus dalhousiensis*, sp. n.
2. Jaw—*A. dalhousiensis*, sp. n.
3. Reproductive organs—*A. dalhousiensis*, sp. n.
4. Chitinous processes inside the penis—*A. dalhousiensis*, sp. n.
5. Penis and dart-sac everted—*A. dalhousiensis*, sp. n.

### PLATE II.

Fig. 6. Shell—*Anadenus lahorensis*, sp. n.
7. Jaw—*A. lahorensis*, sp. n.
8. Reproductive organs—*A. matthaii*, sp. n.

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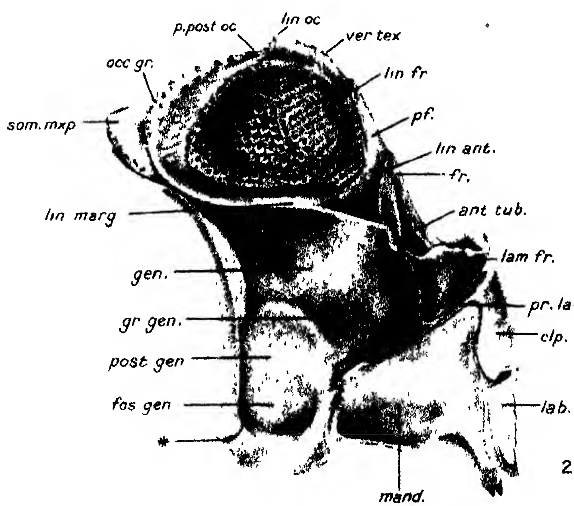


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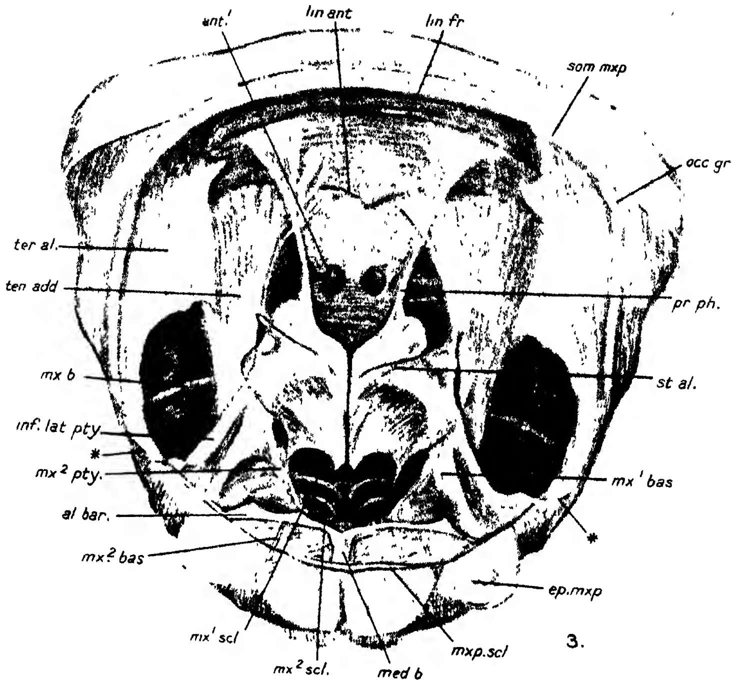
THE MORPHOLOGY OF THE ISOPOD HEAD.

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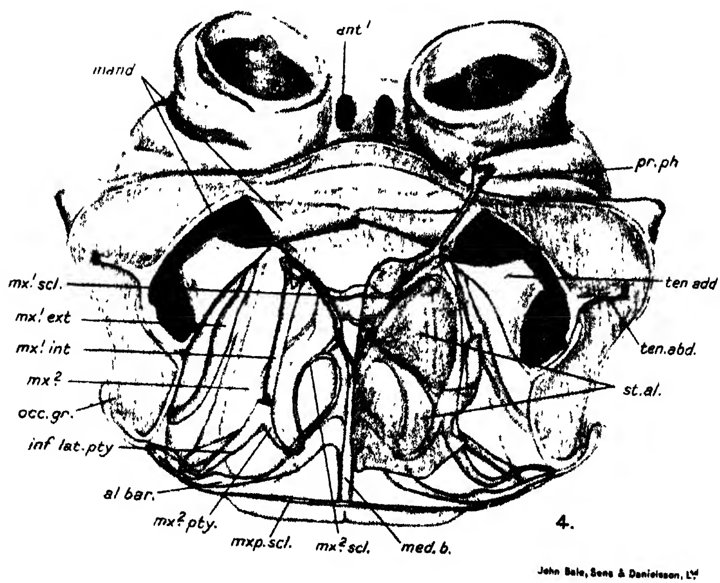


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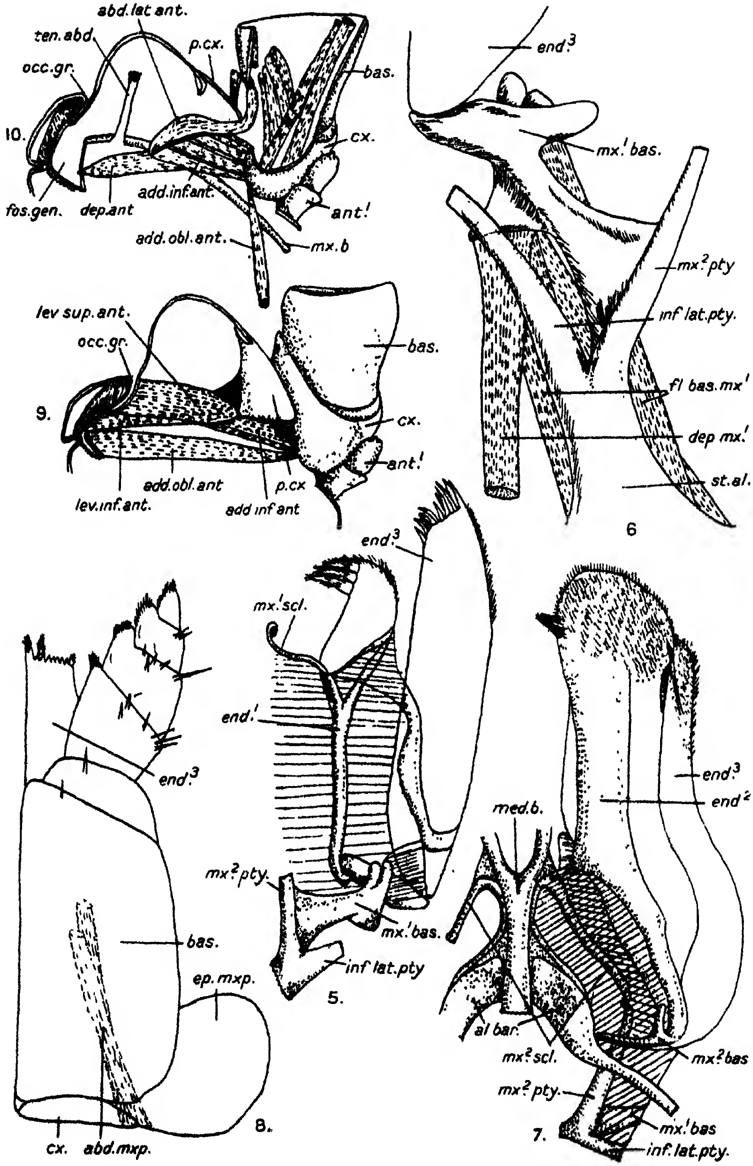


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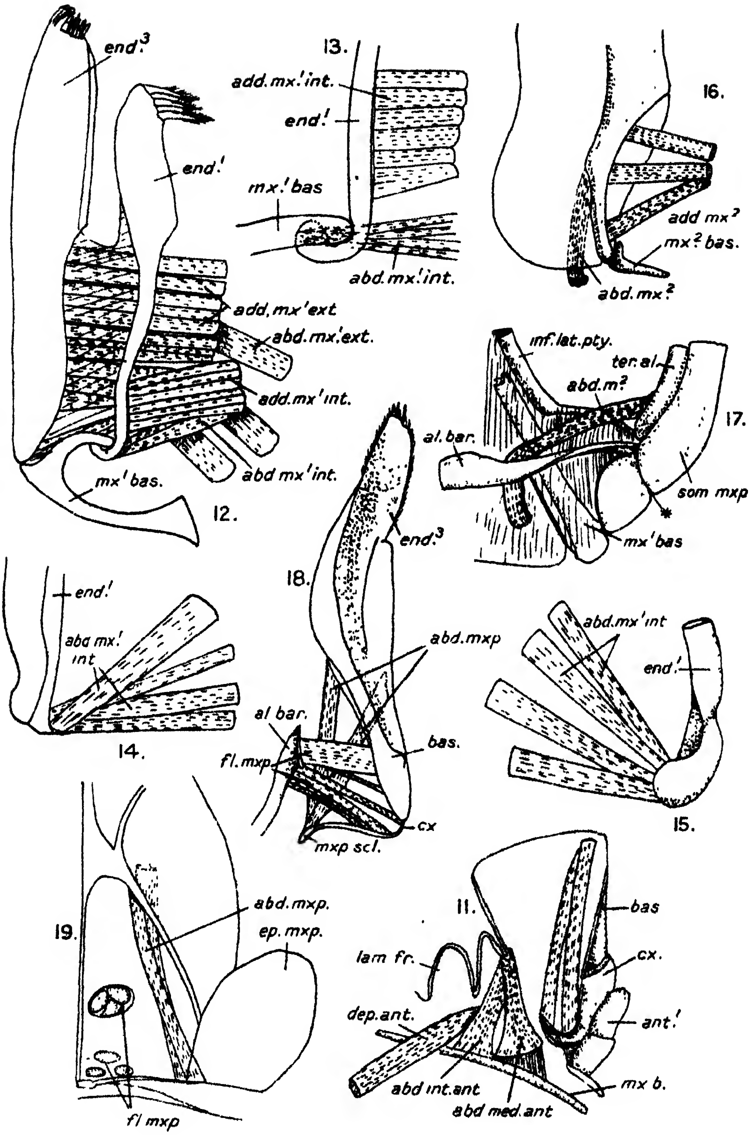


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THE MORPHOLOGY OF THE ISOPOD HEAD.

# 44. The Morphology of the Isopod Head.—Part I. The Head of *Ligia oceanica*. By Harold G. Jackson, D.Sc., F.Z.S., Birkbeck College, University of London.

[Received April 27, 1926: Read June 15, 1926.]

(Plates I.–IV.; Text-figures 1–11.)

Contents.



## 1. *Introductory.*

This study of the Isopod head was undertaken in the first place to provide a uniform terminology of the external structures employed by systematists in descriptions of Terrestrial Isopods. It became evident in the course of the work that, in addition to the Oniscoidea, a survey of nearly related Isopods was necessary to determine the homology of these structures on fundamental anatomical features.

The Terrestrial Isopod which, without any doubt, is the most primitive of the tribe is the genus *Ligia*, and it is fortunate that this genus exhibits, at once, practically all the structures which are found in varying degrees of development scattered among the more highly specialized forms, and by that fact and its relatively large size it is peculiarly favourable as a starting-point for this study.

As it seemed probable that the external form of the head would be correlated with the internal skeleton and the origins of the appendage muscles, these have been worked out, but, although the results are interesting and promising, it is early to make any generalizations on the point. The second part of this study will deal comparatively with the other Terrestrial Isopods and typical aquatic forms.

The author would like to acknowledge here his indebtedness to Dr. W. T. Calman, F.R.S., for his stimulating interest and his constructive criticism and advice.

*Previous work.*—The work of Schöbl (1860) and Sars (1867) is mentioned in connection with the internal skeleton of the head. The external features have been dealt with piecemeal in Budde-Lund's 'Isopoda Terrestria' (1885), but only accustomed travellers in that arid country can interpret the cryptic signs scattered by the way. As far as possible, his terms will be used as a basis for the terminology proposed in this paper, so that the only indispensable book on the Terrestrial Isopods will not be made, at any rate, less intelligible. Dollfus in a serial paper (1888–1892) dealt with the head and general morphology of *Porcellio*, *Armadillidium*, and other Isopods. This work is not without value, but it is probable that it was written rather from the naturalists' point of view than as a critical account for specialists, and the morphological statements in it are often indefensible and unsubstantiated. Hansen's paper on the Cirolanidæ (1890) was a land-mark in accurate description, but no especial study was given to the head. Milne-Edwards and Bouvier (1902) gave a fine account of *Bathynomus*, added to by Lloyd in 1908. The most elaborate account of an Isopod head, which is also well illustrated, is that of Tait on *Glyptonotus* (1917).

*Methods.*—The work has been carried out by means of dissections of freshly preserved material under a binocular microscope with a Pointolite illumination. The skeletal structures have been studied by means of cold potash preparations cleaned by washing with dilute glycerine, as recommended by Hansen for mouth-parts. Such preparations stained with picrocarmine show the detail of the sclerites with great precision. Serial sections cut in collodion and paraffin-wax and stained by Mallory's triple stain or Hæmatoxylin and Eosin (less good for this purpose) were helpful in studying the smaller heads, but the extremely refractory material makes such preparations of the thick chitinous head of *Ligia* unreliable and only of value for confirmation of small points difficult to make out with certainty by dissection.

## 2. *Terminology.* (Plate I. figs. 1 & 2; text-figs. 1, 2, & 3.)

It will be convenient to lay down in the beginning the terminology which will be employed in this paper and discuss the terms used and the significance of the structures named later on.

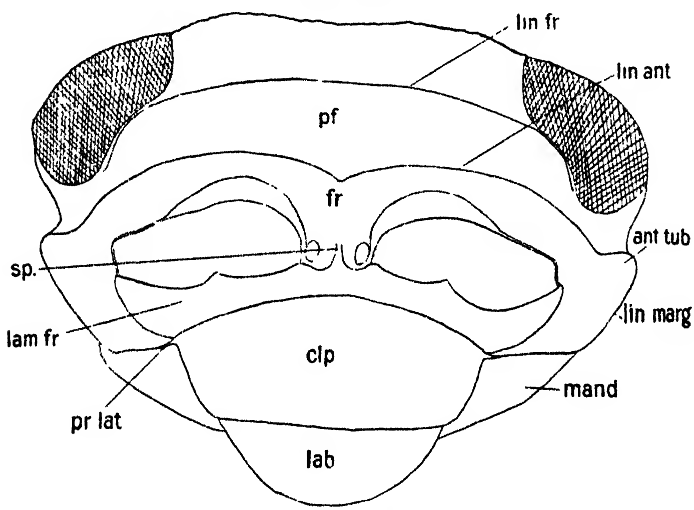
In its natural position seen from above, the head of *Ligia oceanica* is an elongate oval rather more than twice as broad as long. The very large eyes at each end of the oval are separated by a distance of about twice their breadth. The head is partially sunk into a deep concavity on the anterior border of the first free thoracic somite (the 2nd).

On the anterior face the surface falls almost at right angles from the top of the head as far as the insertion of the antennæ

and then slopes rapidly backwards. The most posterior pair of mouth-parts (the maxillipedes) are attached on a line well behind the posterior margin of the top of the head and the remaining parts at varying distances in front of these, but all meet at about the same point just behind the farthest backward limit of the face. They are set at an angle to the face of about 90° (the mandibles have an exceptional position), so that mouth-parts and face together form a strong cone-shaped salient projecting downwards and backwards. The mouth-parts consequently come to be almost vertical in position.

The difficulties of orientation of the head are due to the fact that the greater part of the "face" is formed by the morphological

Text-figure 1.




Outline of Head of *Ligia oceanica* seen from the front.

equivalents of the sternites of the first to fourth somites (ocular, antennulary, antennary, and mandibular), and the mouth of the animal is pushed downwards to open on the point of the downward-directed cone. The sternal elements therefore in front of the mouth are approximately at right angles to those behind the mouth.

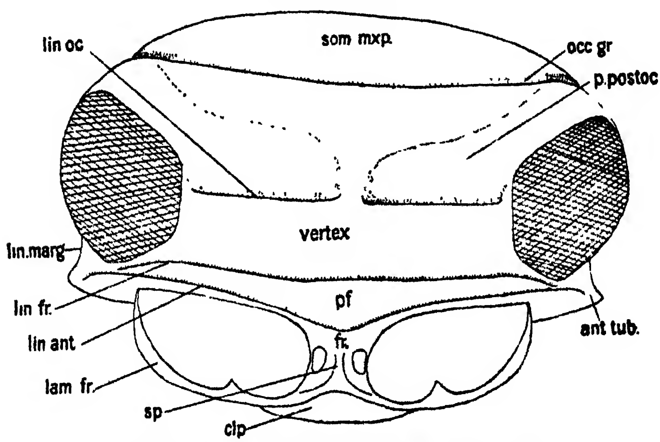
The appendages behind the mouth, in consequence of their nearly vertical position and compressed shape, can without violence be referred to as having an anterior and posterior face, but as this position is not found in all higher Crustacea they will for the sake of clearness be described as having an anterior (inner) and posterior (outer) face and lateral and medial edges.

The head of Isopods is always composed of the cephalon proper

and one or two thoracic somites, for which reason Tait drops the term cephalon in his description of *Glyptonotus* and employs the word "cephalosome." The use of this term in preference to cephalon can certainly be justified, but it has not found general acceptance, and in this paper the custom of the author in previous papers will be followed of preferring the unambiguous and well understood vernacular word for this portion of the body.

Viewed from the dorsal surface (text-fig. 2) a groove is seen to pass over the top of the head near its posterior margin. This groove is shallow medially, but becomes deeper when it passes to the side of the head. It will be called the *occipital groove* (*occ.gr.*), and it separates a narrow posterior part (the *maxillipedal somite*, *som.mxp.*) from the remainder of the head (*cephalon*).

Text-figure 2.




Outline of Head of *Ligia oceanica* seen from above.

From the anterior edge of the groove a well-defined ridge passes forward round each side of the head beneath the eyes. In front of the eyes it passes over a knob which is moderately well defined in *Ligia* (the *antennary tubercle*, *ant.tub.*), and then falls vertically until it reaches the upper margin of the mandible. At this point it turns forward and inward to pass to the front of the face, until it is lost at the junction of the anterior apophysis (articulating peg) of the mandible with the face. This ridge will be called the *marginal line* (*lin.marg.*) throughout its length.

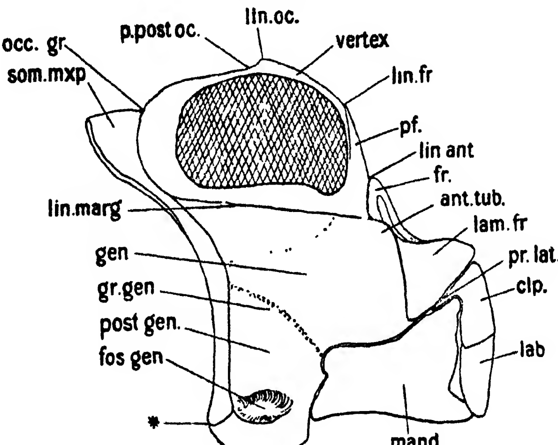
It is not quite clear how much of the marginal line Budde-Lund recognized, but his "linea marginalis verticalis" (the "marginal line of the vertex"—it is not, as has been sometimes assumed, a "vertical" line) seems to include the lateral and posterior portion of the line. In this genus the posterior part

(the anterior margin of the occipital groove) is not as sharply marked as in other genera, where it may form the definitive posterior margin of the head.

On the upper surface of the head between and behind the eyes is a tuberculated area divided into anterior and posterior portions by a sharp ridge (the *interocular line, lin.oc.*). Behind the interocular line are two shallow piriform depressions (the *postocular pits, p.postoc.*), the wide ends of which are directed forwards and separated medially by a narrow ridge: the narrow ends curve backwards and become lost just behind the eyes, inside the marginal line.

The portion of the upper surface between the eyes will be called the *vertex*, following the analogy of the Insect head. The

Text-figure 3.




Outline of Head of *Ligia oceanica* seen from the side.

vertex is bounded in front by a sharp ridge forming a broad arched curve, which passes in front of the eyes and ends blindly a little below them. This is the line called by Budde-Lund "linea frontalis marginalis," and it will be called the *frontal line* (*lin.fr.*). In some genera this line is produced into *lateral lobes* in front of the eyes and into a *median lobe* in the mid-line.

Passing to the face, which is smooth and not tuberculated like the dorsal surface of the head, there will be found beneath the frontal line another well-marked ridge which is marked by a sharp downward angle in the mid-line and on each side passes on to the surface of the antennary tubercle where it becomes lost. This is referred to by Budde-Lund as "linea transversa epistomatis," but, as the term "epistome" will be dropped for reasons

given below, the term *supra-antennal line* (*lin.ant.*) will be used.

The area between the frontal and supra-antennal line will be called the *profrons* (*pf.*).

Below the supra-antennal line is a region which contains the antennular and antennal sockets. The upper part of this region, defined below by the upper margin of the antennal sockets, passing between them and including the antennular sockets, will be called the *postfrons* (*fr.*) †. The projecting shield under the antennæ and including their sockets, which in the mid-line is produced into a small rostrum fused with the frons, is the *frontal lamina* (*lam.fr.*) ‡.

Attached to the ventral limit of the frontal lamina but produced upwards so as to overlap it is a firm plate, the *clypeus* (*clp.*). The upper lateral corners of the clypeus are produced into small *lateral processes* (*pr.lat.*), under which the anterior apophysis of the mandible articulates. Hanging from the clypeus is the semi-membranous *labrum* (*lab.*).

The side-walls of the head are made up on each side of single plates bounded in front and above by the marginal line and behind by the maxillipedal somite. The more anterior portion of the ventral boundary is formed by the mandible and the plate is continued downwards behind the mandible to form a deep flap. This plate is the *gena* (*gen.*) and a light depression (the *genal groove*, *gr.gen.*) passing from the upper posterior angle of the mandible obliquely upwards and backwards divides the plate into an anterior and upper genal part and a posterior and lower *postgenal* (*postgen.*) part. A deep pit in the postgenal part is the *genal fossa* (*fos. gen.*).

The structures on the ventral surface of the head will be dealt with later.

### 3. *The Maxillipedal Somite.*

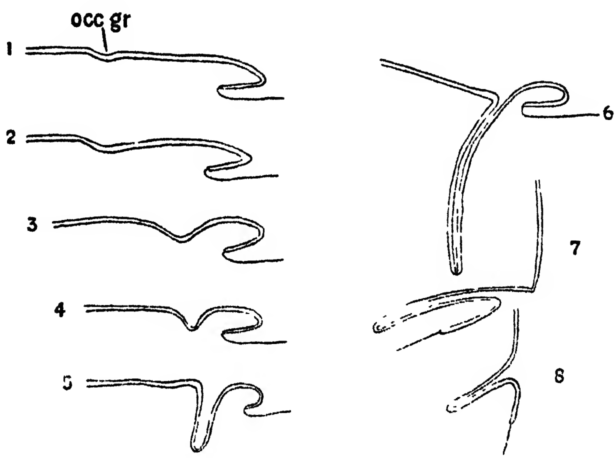
If a continuous series of sections be taken through the occipital groove (text-fig. 4), it will be found that in the mid-line of the dorsal surface the groove is very shallow, but as it is followed to the side it becomes deeper until it forms on each side (viewed from within) a projecting vertical lamina which gives origin to a number of muscles (Pl. II. fig. 3, *ter.al.*). These laminæ were termed the *tergal alæ* by Lloyd, and are seen in section to be invaginations of the external surface. The invagination can be followed to a point behind the genal fossa on each side (text-fig. 3; Pl. II. fig. 3; Pl. IV. fig. 17, *), where the alar bar (*al.bar.*) meets the inner side of the head. The narrow chink at * is a lateral continuation of the invagination and is further continuous

† In those Isopods in which the supra-antennal line is absent, the postfrons and profrons will be said to be confluent and the whole area called the *frontal area*.

‡ To avoid confusion it should be pointed out here that Dollfus mistakenly calls the 1st antenna the "antenna" and the 2nd antenna the "antennule," and attributes the large antennæ to the 2nd cephalic somite and the vestigial antennulæ to the 3rd cephalic somite.

ventrally with a deep membranous crease in the soft chitin, which passes right across the head to meet the similar chink * on the opposite side. In other words, a complete ring is separated off from the posterior part of the head by a groove which is shallow dorsally, very deep laterally, and moderately deep ventrally. The alar bar can be seen in section to be a chitinisation of the upper edge of the ventral membranous crease and therefore equivalent in origin to the tergal alæ (text-fig. 5). The membranous anterior (inner) faces of the maxillipedes are attached immediately

Text-figure 4.




Series of sections through the occipital groove 1, median sagittal; 2–5, successively more lateral; 6 dorsal-lateral margin; 7 and 8 lateral.

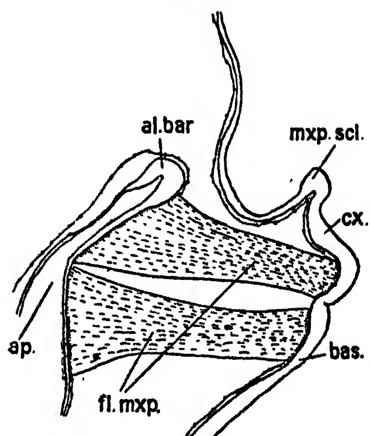
behind the alar bar and the anterior vestige of their sternite is seen, by comparison with marine Isopods, to be fused with it. On the anterior side of the alar bar and the ventral crease are the articular sockets of the maxillæ, which are thus separated from the maxillipedes by the alar bar and the ventral crease.

It seems justifiable to conclude, therefore, that the continuous occipital groove and the ventral crease represent an intersomitic apodeme, and that the posterior portion of the head thus marked off with its paired appendage (the maxillipedes) represents the coalesced first thoracic somite. The tergal alæ would then be interpreted as endopleurites and the alar bar as an endosternite.

This view is put forward with due regard to the fact that Calman (1917) has stated that "the cephalothoracic tergal boundary is coincident with, and is obscured by, the origin of the carapace fold" in all Crustacea but *Bathynella* and the Anostracous Branchiopoda. In the case of *Ligia*, the conclusion

that the occipital groove is intersegmental is so tempting as to outweigh the consideration that in most cases a vestigial carapace fold is apparently involved in the coalescence with the head. A somewhat similar groove is found in the Idotheidæ and in *Bathynomus*, where it is deepened into a cleft laterally even if it is obscured or absent dorsally. In *Glyptonotus*, where two somites are fused with the cephalon, Tait describes two such grooves continued internally (laterally) into arthrophragms between the

Text-figure 5.




Longitudinal section through alar bar and maxillo-maxillipedal apodeme (*ap.*) at base of maxillipede in the plane of the flexor muscle (*Oniscus asellus*).

presumed boundaries of the somites. Their continuity with the ventral apodeme has not, however, been demonstrated.

The term "occipital groove" has been deliberately chosen to indicate a groove separating the cephalon from the mesosome (1st thoracic somite), as the usual term "cervical groove" is not believed by Calman necessarily to indicate any such division (1909, p. 256), and is in any case used in different senses by authors.

4. *The Morphology of the Anterior Somites and their Terminology.*

The term "epistome" has been applied in the Decapoda by Milne-Edwards to the sternum of the antennary somite. Huxley (1880) suggests that in the Crayfish this structure appertains in part to the antennal and in part to the mandibular somite. It is necessary to find out how far this condition might correspond with that in the Isopoda.

In *Ligia* the antennary sockets are very large, and are bounded below by a shield-like plate (termed by Hansen the "frontal

lamina"), which passes continuously across the face from one socket to the other (text-fig. 1; Pl. I. fig. 1, *lam.fr.*). This plate is continued upwards in the medial aspect of the sockets to form a scimitar-shaped sclerite which can be followed round the socket as a narrow rib until it rejoins laterally the frontal lamina. In the mid-line the lamina is produced to form an upward-directed spine (*sp.*), which separates the antennular sockets and becomes smoothly fused with the postfrons. (In *Idotea* and related genera, the spine is not confluent with the face.) The term frontal lamina must therefore be applied to a structure which includes the antennary sockets. The frontal lamina is based on a thick chitinous rib (the *maxillary bar*, Pl. II. fig. 3, *mx.b.*) which runs right across the front on the inner side of the cranium, ending at a point on each side where the posterior apophysis of the mandible is inserted in the gena. Below the frontal lamina and depending from the maxillary bar is the somewhat oval clypeus, which is expanded upwards partly to cover the frontal lamina, so that there is a very deep fissure between the two. The lateral processes of the clypeus attain great size in some terrestrial Isopods. The articulation of the anterior apophysis of the mandible with the clypeus and its relationship with the labium below has been taken by Bourne (in Decapoda) and various authors (in Isopoda) to demonstrate the identity of this structure with the mandibular sternite.

Similarly, it may be argued with some probability that the frontal lamina and chitinous sockets of the antennæ represent, at any rate, some portion of the sternite of the antennary somite.

The backward migration of the antennulæ, so that they come to lie between the usually widely-spaced antennæ, which is such a prominent feature of the terrestrial Isopods, has made it a matter of great difficulty to identify any part of the somite to which they belong. Even the surmise that it may be bounded above by the supra-antennal line is not without danger, as this line is prone to disappear in many genera.

It will be seen then that, on these homologies, the term "epistome" of the Decapoda is applicable, if at all, with the frontal lamina, but as the application of this term is so varied in Decapoda (as pointed out by Bourne (1922)), and in Isopods has been applied indiscriminately to the whole or part of the "face," it seems better to drop it altogether. It is therefore proposed above to retain the term frontal lamina, to call the area containing the antennulary sockets the postfrons, and the area above the supra-antennal line and below the frontal line the profrons.

Milne-Edwards and Bouvier (1902) come to different conclusions from these as to the interpretation of the anterior somites. The frontal lamina is alternatively termed "ou segment antennulaire" and the clypeus "ou segment antennaire," but no

evidence is given for these assertions, which, on the face of it, do not seem likely.

Dollfus, in the papers referred to (1888–92), divides the face into three parts, prosepistome, mesepistome, and metepistome on a study of the heads of the specialised wood-lice *Porcellio* and *Armadillidium*. The divisions between the parts are far from clear, although he introduces in his figure of the head of *Porcellio* sp. (no. 237) a dividing-line which has no existence in any *Porcellio* seen by the author, and is only called for by his erroneous assumption that the antennulary somite is the 3rd and not the 2nd of the head. His metepistome is the clypeus, and in a categorical statement he refers to it as the mandibulary sternum (probably correctly), and the others (undoubtedly incorrectly) as the antennary and antennulary somites respectively (see footnote on p. 890 above). These terms, which are very indefinite and founded on very doubtful homologies, would, therefore, be better abandoned.

It remains to discuss the propriety of introducing terms from such a highly specialised group as the Insects. The head of an Isopod or Amphipod and an Insect has been considered by many authors to consist of the same number of somites, and Hansen (1893) has not hesitated to compare, segment by segment, the maxillæ and labium of *Machilis* with the maxillæ and maxillipedes of the Gammarinæ. Both heads have their lateral parts made up of a single sclerite, which in both receives the posterior apophysis of the mandible and is bounded above by the vertex, so it seems reasonable not to duplicate terms but accept for the Crustacean the term gena. It is also convenient to adopt the term postgena for a partially separated-off postero-ventral portion of the gena. The fact of the articulation of the anterior apophysis of the mandible and the relations of the labium with the clypeus makes its name suitably parallel with the similar region of the Insects, and, although the morphological equivalence may not be thereby exactly demonstrated, it is at any rate suggestively similar.

In the Insect there is usually no actual division between clypeus, frons, and vertex, although the areas are fairly clearly defined. In *Ligia* the region called "frons" in the Insect is divided into three areas, and the necessity arises of distinguishing between them. The name frontal lamina having already been applied to the lowest division, it seemed convenient to qualify the term "frons," and postfrons is suggested accordingly for the middle region and profrons for the uppermost division.

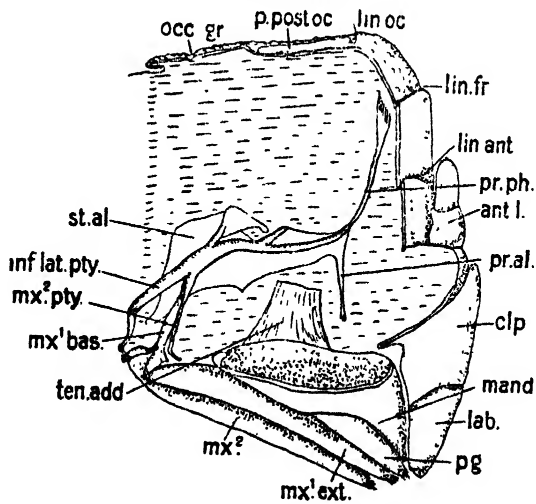
The terminology of other authors is far from clear. Budde-Lund seems to use the term epistome for the area between the clypeus and the marginal line, frons for the area between the eyes, and vertex for the back of the head. This terminology is obviously unsuitable, as if terms from entomology are used they must be used in carcinology with as near as possible a similar meaning. Budde-Lund's frons is the vertex of entomological

usage and his vertex the occiput. The term "epistome" has not been used in entomology. Dollfus seems to use the term "vertex" as equivalent to his prosepistome—the other extreme to Budde-Lund. The genal region is called by Dollfus "pleural," and divided into epimerienne (=genal) and episternale (=postgenal), and the division between them the "fossette pleurale" (=genal groove). The term "epimeral" is, however, as indefinite and objectionable as "epistome."

### 5. *The Inner Surface of the Head-capsule.*

On the inner side of the "face" the frontal and supra-antennal lines are seen as well-marked grooves (Pl. II. fig. 3). The antennular sockets are seen obviously to belong to the area bounded above by the supra-antennal line and below by the upper boundary of the antennal sockets. The scimitar-shaped upper margin of the antennal sockets is continued downwards into stout rods, which pass below into the frontal lamina. The

Text-figure 6.




*Ligia oceanica.* Skeletal structures in connection with the Right Maxillula. The right side of the head as far as the nearest antennary socket, the maxillipedes, and part of the mandible removed.

median rostrum of the frontal lamina is seen as a crease. The frontal lamina is projected well forwards beneath the sockets and on its inner edge joins the very stout, curved, maxillary bar. Underneath the maxillary bar on each side lie the mandibles, along the whole upper edge of each of which is a glenoid surface working on the maxillary bar, so that they swing on it and on their apophyses as from a hinge. A light rib (genal groove) on

the gena continues the bar obliquely upwards until it reaches the margin of the mandibular somite. A further rib, strengthening the gena, is to be found above this running from the point the genal groove reached on the maxilliped somite to a point below the marginal line in front of the eye.

This system of stout girders and ribs is brought into being by the stress exerted by the powerful adductors of the mandibles, which tend to collapse the capsule inwards. The clypeus is seen as a deeply concave plate resting above on the maxillary bar, and hanging under it is the pocket-like labium.

The occipital groove is seen on the dorsal aspect as a slight rib, which deepens till it forms on each side the prominent tergal alæ. These gradually diminish by the genal fossæ, which form prominent flattened bosses on each side.

The remaining ventral structures will be dealt with in connection with the mouth-parts and endophragmal skeleton.

### 6. *The "Maxillo-sternal" and Endophragmal Skeleton.*

The skeleton of the head in connection with the mouth-parts in Isopods is of an unusual complexity. The simple and easily interpreted succession of sternites found in more generalised forms which retain the caridoid facies has given place to an elaborate framework in which nearly all trace of the original segmentation has been lost. The apparatus was apparently first described by Schöbl (1860), who gives a good but incomplete figure of *Haplophthalmus*, which has obviously much in common with *Ligia*. Sars (1867) figures and describes the same apparatus in *Asellus aquaticus*, in which it seems to be simpler than in other Isopods, but he attempts no interpretation of the structures figured. Dollfus (1888–1892) gives incomplete and semi-diagrammatic figures of *Armadillidium* and *Porcellio*. Milne-Edwards and Bouvier (1902) figure it for *Bathynomus*, and give doubtful interpretations of the structures, and this account has been added to by Lloyd (1908). Finally, Tait (1917), with favourable material, has given a full account of the internal skeleton of *Glyptonotus*, but the correspondence with that of *Ligia* and *Bathynomus* does not seem to be exact enough to make it possible to employ all Tait's terminology.

In such a form as *Bathynomus* the removal of the oral appendages reveals a succession of sockets which incline inwards from the widely divaricated mandibular sockets in the front to the closely applied maxillipedal sockets behind. The sockets are divided by membranous or chitinous bands, and the sclerites formed between the maxillulary and maxillary sockets are attached to a median antero-posteriorly running bar which seems to show definite evidence of segmentation.

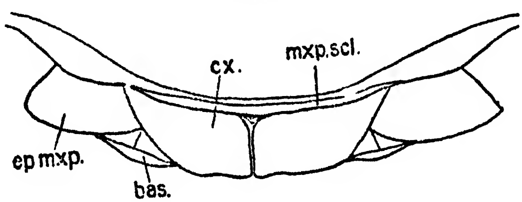
In *Ligia* this orderly arrangement is obscured by the backward migration of the maxillulæ to the side of and almost behind the maxillæ, until their basal parts come to lie on either side of

the maxillipedes, between them and the lateral part of the cranium. The difficulty of demonstrating any segmental arrangement is increased by the absence of any trace of divisions in the median bar, which is fused into a single piece.

*Maxillo-sternal Framework.*—The ventral side of the head-capsule in *Ligia*, which bears the oral appendages, is mostly soft uncalcified chitin, but a system of calcified bars is developed in the chitin, forming attachments for the bases of the oral appendages and, in the case of the maxillipede, the origin of its muscles. An apparatus is thus formed which consists of a median longitudinal bar from which spring a number of paired rods. The rods are hollow and open to the exterior throughout their length, being essentially chitinisations of the upper edges of deeply invaginated creases.

As seen from inside the head and above (Pl. II. figs. 3 & 4), the most prominent feature is the median bar (*med.b.*) which is heavily calcified and slightly grooved on its inner (dorsal) surface for a great part of its length. Its extreme posterior limit is

Text figure 7.




*Ligia oceanica.* Maxillipedes *in situ* seen from the posterior aspect.

behind the base of the maxillipedes, where it supports a slender T-piece (the *maxillipedal sclerite*, *mxp.scl.*) to which the coxa of the maxillipede is attached.

Owing to the coxa being bent at right angles to the basis its attachment is thrown above that of the other appendages, and the median bar dips sharply downwards between the maxillipedes before turning forwards in a parallel course to the distal portion of the maxillipede and the other appendages. It divides before reaching the base of the paragnaths, a branch passing into each paragnath and forming its sickle-shaped skeletal support. A slender process just above the entry of the bar into the paragnaths passes upwards and is attached to the anterior part of the cranium by membranous attachments on either side of the œsophagus and buccal framework, at the point where the anterior apophysis of the mandible engages with the clypeus.

At the posterior end of the bar in front of the maxillipedal sockets it is joined on each side by a large sclerite which superficially appears spoon-shaped, the bowl facing backwards on each side of the median bar and handle curving back to join the head

just behind the genal fossa. The paired structure is the *alar bar* (*al.bar*) of Lloyd, and it has been pointed out above that it is a chitinisation of the upper edge of the deep crease which is a ventral continuation of the occipital groove. In the spoon-like concavities at the medial end of the bars originate the maxillipedal muscles.

It has been stated above that maxillipedal elements enter into its composition, as is shown by a comparison of the condition in *Ligia*, where only the posterior margin of the maxillipedal socket is defined by a sclerite, and in *Idotea*, *Glyptonotus*, and *Bathynomus*, where it is also defined anteriorly, so that a distinct though vestigial sternite is present.

The maxillary arthrophragm (*mx*$^2$.*scl.*) originates from the alar bar at its narrowest part and runs inwards, bound up with, but distinctly separable from, the bar until it turns forwards and reaches the level of the branches to the paragnaths. It then becomes separate from the median bar and curves backwards to return to its point of origin, but instead of rejoining the alar bar it turns sharply upwards to the internal skeleton of the head. This incomplete circle forms the base of the membranous attachment of the maxillæ.

At the anterior end of the median bar, just before the two diverticula enter the paragnaths, a sclerite with a knob-like end is movably articulated with each diverticulum, but held in place and limited in movement by a chitinous connection with the skeleton of the paragnaths. It passes laterally outwards almost at right angles to the median bar, diverges from the paragnath skeleton, and turns sharply downwards to become attached to the inner (anterior) face of the inner endite of the maxillula (*mx*$^1$.*scl.*). At the sharp bend there is a notch which appears to allow a hinge-like motion and just beyond the bend a slender sclerite is given off which passes to the lateral border of the inner endite and defines its free distal portion. This *maxillulary sclerite* forms the anterior boundary of the maxillulary socket, which is bounded medially and behind by the maxillary sclerite and the maxillary pterygoid process and laterally by the lateral pterygoid process and the mandible. Schöbl figures this sclerite in *Haplophthalmus* and Dollfus in *Porcellio* and *Armadillidium*, and the author has found it in every Isopod examined, but it is not figured or described in other accounts and may have been missed. Its function will be dealt with in connection with the muscular system.

*Endophragmal Skeleton* (Pl. II. figs. 3 & 4).—The endophragmal skeleton of the head seems to differ considerably from that of *Glyptonotus*, and it is difficult to follow Tait's account from the structures in *Ligia*, or, for that matter, to correlate it with Lloyd's account of *Bathynomus*, which approaches *Ligia* more nearly.

The skeleton in *Ligia* arises from a slit-like invagination on each side of the ventral surface immediately in front of the alar

bar. The soft integument is drawn inwards and slightly forwards to form on each side a cone, very much flattened antero-posteriorly, and with its lateral and medial edges strengthened by stout chitinisations. Of these four calcified chitinous bars the two lateral (*inferior lateral pterygoid processes, inf.lat.pty.*) are attached to the side-wall of the cranium immediately anterior to the point where the alar bar and groove pass into the occipital groove. Lloyd conjectures that in *Bathynomus* they are "derived from" the alar bar, but this is not so in *Ligia*, and is in any case unlikely. The two medial (*maxillary pterygoid processes, $mx^2$.pty.*) pass inwards and downwards as it to join the alar bar, but becoming continuous with the maxillary sclerite, as described above, they really are only held in position by the spring-like action of this almost spirally-twisted bar.

Running in the anterior wall of the "cone" is the proximal segment of the maxillula (*$mx^1$.bas.*), which passes upwards and expands to become firmly fused with the maxillary pterygoid process just before it joins the lateral pterygoid process at the top of the cone. The appearance from behind is rather like a three-legged easel draped with semi-transparent muslin.

By the nature of their origin the two pterygoid processes are semi-tubular, but at the top of the cone the half tubes join to form a single tubular rod passing forwards which expands backwards and forwards into a thin chitinous plate, which in the natural position of the head is almost parallel to the ground (Pl. II. figs. 3 & 4; text-fig. 6, *st.al.*). A shallow groove marks off an anterior from a posterior portion of the plate. The whole structure on both sides forms an irregular table, the anterior portion of which is well supported by the pterygoid process and the posterior part membranous and ill supported. It may be called by Lloyd's name, the *sternal alæ*.

The hind border of each sternal ala is curved downwards and ends in two points, the lateral one of which is attached to an exceedingly slender rod arising from the alar bar. Each is also curved downwards along its medial border, which is almost linear, and the borders are united by fibrous material, so that the combined alæ form a platform on which the gizzard rests and underneath which the nerve-cord runs. The anterior edges of the alæ are also reflected downwards and bear a light tendinous process (*pr.al.*) on each side, which passes in front of the great adductor tendon of the mandible and gives origin to a group of six small muscles, which spread out and are inserted on a line just below the posterior apophysis of the mandible on its inner surface. Both alæ have the anterior medial margin excavated so as to form a U-shaped depression to allow of the passage of the œsophagus. On either side of the œsophagus two chitinous rods arise from the anterior margin which pass almost vertically upwards to become attached by a fan-shaped insertion to the inner surface of the vertex immediately above the frontal line

just to the inner side of the eyes. The point of attachment is marked on the exterior by a slight depression * (*pr.ph.*).

These *pharyngeal processes* hold the sternal alæ in the front and take the strain of the adductors of the maxillulæ and maxillæ which originate from them.

By the nature of their development all the structures described above consist of a double layer of chitin.

The median ventral bar in *Ligia* shows no trace of the segmentation observed in *Bathynomus* and *Glyptonotus*. In the figure of the sternal structures of *Bathynomus*, Milne-Edwards and Bouvier (1902, pl. iv. fig. 9) identify the sternites of the two maxillary and the maxillipedal somites by this segmentation, but the figure does not give any confidence as to the accuracy of this determination. The mandibular sternite is identified with a narrow bar on each side, which can be almost exactly paralleled in *Ligia* in position and shape by the maxillulary sclerite. The authors were bound to seek the mandibular sternite here, as they had identified the clypeus as the antennary sternite, but if this parallel with *Ligia* is correct it is certainly an error, and it must in any case be extremely doubtful.

It remains to discuss the morphology of the structures described above. It has been suggested that the alar bar is homologous with the endosternite between maxillary and maxillipedal somites, but it is more difficult to suggest any homology for the remainder of the endophragmal skeleton. It obviously belongs to the two maxillary somites, as it is found in that position and is the origin of the adductor muscles of the appendages.

Its development as a paired invagination on each side, and the fact that the invagination is continuous with the crease on which the maxillary sclerite runs, suggests that the crease is in the position of a dividing apodeme between maxillulary and maxillary somites, and when it is recollected that the appendage of the maxillulary somite has passed to the outer side of the maxilla the ∩-shaped line of division between the somites becomes intelligible. It is also obvious on this hypothesis that the maxillary sclerite (the anterior sternal margin of the socket of the maxilla) should be continuous with the maxillary pterygoid process and not with the alar bar.

If this interpretation be correct, the endophragmal structures arising from the crease may be looked upon as the endosternite

* It will perhaps save confusion to readers of Tait's paper to point out here that he has misread Lloyd's description of these structures. Lloyd clearly means by "anterior portion of the plates" the structure described above by a similar term and what Tait seems to call the "alar plate," and he rightly asserts that this anterior portion gives origin to muscles of the foregut. He goes on to refer to the chitinous rods described above as forward continuations of the anterior portion of the plate, which Tait calls the "pharyngeal processes" (a term which will be adopted). Tait, however, credits Lloyd with meaning by "anterior portion of the plate" his "pharyngeal processes" and with asserting that these slender bars give rise to foregut muscles, an interpretation which is certainly erroneous.

(characteristically not united in the mid-line) dividing these two somites. It would then be on all fours with the maxillipedal-maxillary endosternite (the alar bar) in forming the origin for the adductor muscles (in the maxillipede, however, named "flexor") of the appendages. The abductors are fixed to the inner side of the cranium, which presumably contains the lost pleural elements of these somites.

## 7. *The Appendages and their Musculature.*

*Appendages.*—The general structure of the appendages of *Ligia oceanica* has been dealt with frequently, and it would be unprofitable to redescribe them, but some comments must be made with respect to their morphological structure. Hansen has pointed out (1890, 1925, etc.) that three segments can often be recognized in the protopodite ("sympod") of the limbs of many Crustacea, and has interpreted the basal segments of the mouth-parts of a number of Isopods from this point of view.

The antenna of *Ligia*, as he has pointed out, has a sclerite which he interprets as the præcoxal segment (Pl. III. fig. 9; *p.cx.*), inserted at its base on the upper and outer side behind the coxa. This segment is not prominent on the outside of the head, but it is prolonged within it to form a large tendinous attachment for muscles.

The maxillulæ have a curiously modified base in connection with the peculiar mechanism of their movement dealt with below. A figure of the same appendage of *Idotea pelagica* is given for comparison (text-fig. 8). It will be seen that *Idotea*, in common with the examples figured by Hansen, has three well-marked basal segments, from two of which, the præcoxa (*p.cx.*) and basis (*bas*), endites arise. The præcoxa articulates freely with the maxillary pterygoid process which is not curved back in a spring-like form. The præcoxal endite (*end*$^1$.) articulates with the præcoxa by a broad condylar surface. The coxa (*c.x.*) is on the way to become vestigial, but it still supports the basis and its large endite (*end*$^2$.).

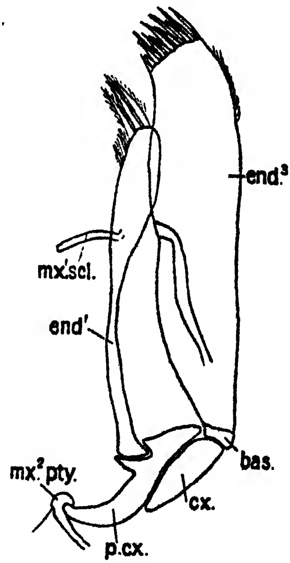
In *Ligia oceanica* præcoxa and coxa are indistinguishably fused together (this view is preferable to believing in the disappearance of the coxa) to form a hammer-shaped sclerite (*mx*$^1$.*bas.*, Pl. III. figs. 5 & 6), which is fixed at its handle-end by a fan-shaped junction to the maxillary pterygoid process (*mx*$^2$.*pty.*). It is therefore capable of no independent motion.

The præcoxal endite (*end*$^1$.) is articulated to the basal sclerite with great freedom and does not work in a socket. Rather it see-saws on a fulcrum formed by a projecting knob of the sclerite working in a condylar surface a short distance from the proximal end of the endite, to which it is loosely bound by a membranous attachment. The supporting sclerite of the endite is curved under the condyle formed by the basal sclerite (Pl. IV. figs. 12 to 15). The object of this arrangement will be appreciated when

the muscles of the maxillula are considered, but it may be remarked here that the endites of this genus have a considerable power of independent motion, although the structure of the appendage in *Glyptonotus* makes it obvious that Tait is correct in attributing "little independent movement of the one lobe relatively to the other."

Just at the base of the broadened head of this endite (*i. e.*, where it projects freely beyond its investing membranes), on the anterior (inner) aspect, comes off the slender rod (the maxillulary sclerite) which articulates with the median bar (*mx*$^1$.*scl.*, fig. 5).

Text-figure 8.




*Idotea pelagica.* Left maxillula from the posterior (lower) aspect.

The position of this sclerite makes it tend to oppose an adductor motion of the endite.

The endite of the basis moves freely on the basal sclerite on the broad condylar surface that is usually found.

The range of action of the whole appendage is limited anteriorly (above) and laterally by the paragnaths and mandibles, on the medial side by a projecting chitinous pad from the median bar and the medial edges of the maxillæ, and posteriorly (below) by the maxillæ, which form shallow gutters tightly enclosing and guiding the maxillulæ. The whole appendage is capable of free up and down movements in its gutter, but little real lateral movement.

The outer endite during feeding is very active and moves

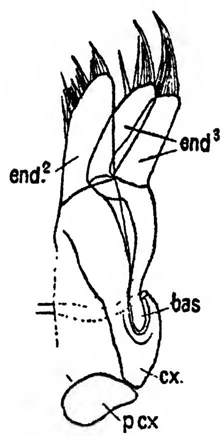
rapidly backwards and forwards, taking the greater part in stuffing the food into the mouth.

The basal segments of the maxillæ are similarly modified by the apparent fusion of præcoxa and coxa into a single sclerite (*mx*$^2$.*bas*., Pl. III. fig. 7, Pl. IV. fig. 16). The basis is entirely membranous, its endite weak, scarcely separated from the coxal endite, and not subdivided. The coxal endite is strongly developed.

The appendage is incapable of much movement, but the slight movements of adduction and abduction are pivoted on the basal sclerite. It seems to take no active part in ingestion of food.

The maxillipedes show no trace of the segment interpreted by Hansen as the præcoxal in some other Isopods. The coxæ are

Text-figure 9.




*Idotea pelagica.* Right maxilla from the posterior (lower) aspect.

articulated to the maxillipedal bar and the bases are bent at right angles to them. It is important to note that the coxal segment is distally rounded, so that the basis can rock upon it (text-fig. 7; Pl. III. fig. 8). Each maxillipede is capable of an upward and downward and a slight lateral movement of this joint. The epipodite is not subdivided and forms a stiff shield over the base of the maxilla. The maxillipedes move little in themselves while feeding, but the endopod has considerable mobility and acts as a tongue for licking soft food towards the maxillulæ.

The mechanism of the mandibles has been adequately described by Tait, and there is nothing to add for this genus to that account.

*Musculature.*—There does not seem to be an account of the muscles of the head of any Isopod, but they are important as

regards their influence on the outside markings of the head and interesting for their peculiar mechanical action. All the more powerful muscles and some smaller ones cause the surface to be indented at their point of origin. Thus the genal fossæ mark on the outside the origin of the great antennal muscles, the post-orbital pits the line of origin of the adductors of the mandibles, a number of small pits on the mandible mark the insertion of the muscles from the membranous attachment of the sternal alæ, and deep grooves in front of the eye mark the point of attachment of the pharyngeal processes of these alæ. On the mechanical side *Ligia oceanica* is remarkable for its disregard of the usual principle of the vertebrate, which it has almost become a habit to assume for all, that every muscle has another muscle as its potential opponent. The adductor muscles of the mouth-parts of *Ligia* are large and powerful, but the abductors are out of all proportion weak and difficult to find. This weakness is compensated for by the mechanical "spring" devices that have been mentioned in connection with the skeletal parts.

The following account is believed to be complete as regards the muscles of the appendages, but it was considered unprofitable and outside the main objective of this paper to describe a number of small muscles in connection with the œsophagus and "gizzard."

The muscles of the *Antennulæ* are small and of no importance.

The *Antennæ* are moved by a large number of muscles with a somewhat complex action which allows of a wide range of motion. From the inner surface of the genal fossa on each side a wide band of muscles passes forward over the mandible between its adductor and abductor tendons to be inserted on the præcoxal and coxal segments. The most dorsal of them is the *levator superior* (Pl. III. fig. 9, *lev.sup.ant.*), which is a very stout muscle inserted on the upper side of the internal production of the præcoxa; the *levator inferior* (fig. 9, *lev.inf.ant.*) lies under superior and originates to its medial side.

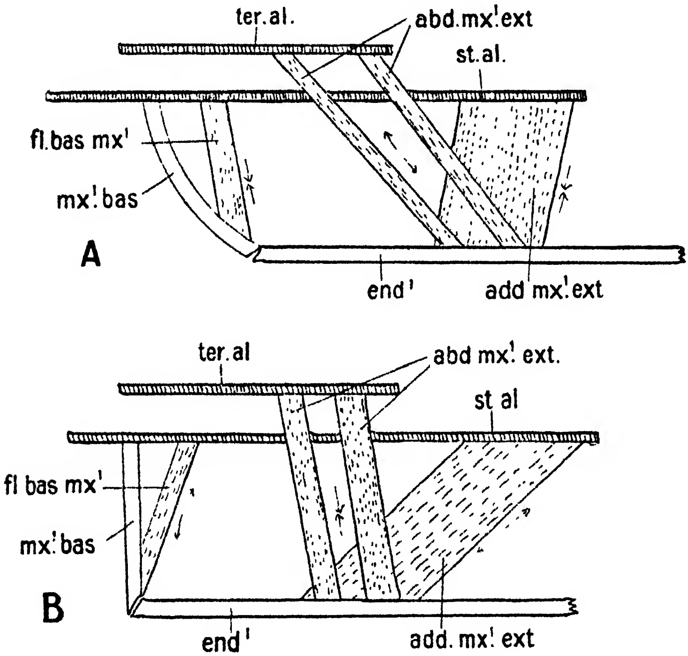
The *adductor obliquus* (figs. 9 & 10, *add.obl.ant.*) originates further to the medial side of the levators and is inserted on the upper side of the base of the coxa. It moves the segment sharply upwards and inwards. The *depressor* (Pl. III. fig. 10; Pl. IV. fig. 11, *dep.ant.*) originates beneath levator and is inserted on the under side of the base of the coxa. It acts in effect as the opponent of levator, although inserted on a different segment.

The main adductor muscle (*adductor inferior*, figs. 9 & 10, *add.inf.ant.*) consists of a number of muscles arising from the inner face of the præcoxal extension, on the outer face of which the levators are inserted. It is inserted on the coxa. The abductors are three in number. The *abductor lateralis* (fig. 10, *abd.lat.ant.*) has a curious origin on the præcoxa on the opposite face to that of the adductor inferior. It passes through the coxa, twisting underneath the incompletely calcified præcoxa, to its insertion on the outer (lateral) side of the proximal part of the basis. The *abductores intermedius* (*abd.int.ant.*) and *medialis*

(*abd.med.ant.*, Pl. IV. fig. 11) originate on the maxillary bar —the latter on a tendinous attachment—and pass beneath the abductor lateralis to a similar insertion below it on the basis. The independent and combined action of these muscles provide for a considerable range of motion, but their action is sufficiently clear from the figures to make a detailed description unnecessary.

The *Mandible.*—The *adductor* has a very extended origin on

Text-figure 10.

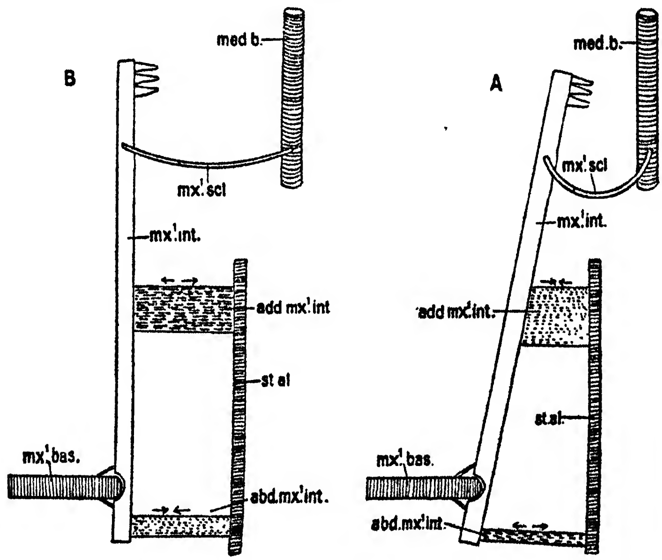



Diagrammatic representation of the mode of action of the outer endite of the maxillula. The movements are reduced to one plane and the independent action of the maxillary pterygoid process ignored. A, adduction; B, abduction.

the inside of the cranium around the eye and almost to the mid-line between the eyes, and on the surface of the tergal alæ. Its tendon is a great fan-shaped structure prominent in preparations of the skeleton (Pl. II. fig. 3, *ten.add.*). The *abductor* is a group of four small muscles, two of which originate on the most dorsal portion of the tergal alæ, one on the marginal line immediately behind the eye and another at the postero-medial angle of the eye. The small tendon is attached near to the posterior apophysis (Pl. II. fig. 4, *ten.abd.*).

The *Maxillula.—Outer (basis) endite*: The powerful *adductor* (text-fig. 10; Pl. IV. fig. 12, *add.mx*$^1$*.ext.*) originates on the under surface of the sternal ala of its own side and takes up most of the ventral surface of the structure. It runs downwards and backwards, becoming more compact, and is inserted in the fossa at the medial border of the endite. The *abductor* (*abd.mx*$^1$*.ext.*) consists of two or three muscles which originate widely on the front edge of the lateral tergal ala. The narrow bands approximate as they pass downwards and a little forwards to their insertion at the lateral side of the adductor. Movement of this endite, which is

Text-figure 11.




Diagrammatic representation of the mode of action of the inner endite of the maxillula. The movements are reduced to one plane and the maxillary sclerite is represented as a simple "spring" and its "hinge" motion ignored. A, adduction; B, abduction.

very vigorous, involves movement of the whole appendage, hence the adductor may be considered to act for both endites as far as a general forward and inward movement is concerned. Similarly, the weak adductor opposes it for the whole appendage, as will be explained below.

However, the *inner* (*præcoxal*) *endite* has independent movement. Both *adductor* (figs. 12 & 13, *add.mx*$^1$*.int.*) and *abductor* originate on the ventral surface of the tergal ala of its own side. The former is a relatively powerful muscle, which is inserted to the distal side of the articulation of the endite with the basal sclerite.

It works against the maxillulary sclerite, which tends to bring the endite back into position and thus aid the weak abductor. The *abductor* (Pl. IV. figs. 12 to 15, *abd.mx*[1]*.int.*) consists of four or five bands of muscle, which are inserted on the knob-like proximal extremity of the endite below the glenoid cavity for the reception of the process of the basal sclerite. The opposing muscles therefore rock the inner endite on the fulcrum provided by the basal sclerite. The maxillulary sclerite, besides aiding abduction, helps to hold the endite away from the head and keeps the condylar surfaces between the basal sclerite and the endite in close opposition (text-fig. 11).

The basal sclerite has a number of muscles of its own (*fl.bas. mx.*[1], Pl. III. fig. 6). These originate as parallel bands from the sternal ala just beyond the point where the maxillary pterygoid process and the lateral pterygoid process meet, and are inserted on the distal end of the basal sclerite. Another muscle (*dep.mx.*[1]) originates on the tergal ala and is inserted on the lateral part of the basal sclerite. This muscle tends to raise the proximal end of the appendage and thus depress its distal end, an action which is opposed by the adductor which acts upwards as well as forwards and inwards. The other muscles are only intelligible taking into account the movement of the entire appendage.

If a macerated cranium be taken and the flesh cleaned out of it by gentle washing, the skeleton appendages lie free in their normal positions. If now a fine needle be inserted into the adductor fossa of the outer endite and the appendage drawn forwards in its groove and then released (see p. 902), it will spring smartly back to its former position by virtue of the action of the semi-spiral maxillary bar and the flexion of the basal sclerite itself. In the living animal the adductor takes the place of the needle, but the spring resistance of the maxillary sclerite and the basal sclerite is strong and the adductor is aided in overcoming it by the bands of muscle which pass down the anterior face of the basal sclerite and come into play immediately it tends to be bent in their direction (text-figs. 6 & 10). (It should be noted that the terms "adduction" and "abduction" are necessarily used loosely in connection with the oral appendages. The sickle shape of the outer endite makes approximation of the biting-tips possible by a forward movement of the whole appendage, consequently the adductors assert a forwards and inwards and not merely an inwards pull.)

The diagrammatic representation of this action (text-fig. 10) necessarily reduces the movements to one plane and does not take into account the maxillary sclerite on the medial side of the appendage. This is so placed as to tend to draw the proximal end of the appendage towards the mid-line when the basal sclerite is bent forwards and thus withdraw the curved outer endite along its groove in a more effective fashion than would be possible with a straight backwards pull.

The *Maxilla* (Pl. IV. figs. 16 & 17).—The musculature of this appendage is weak and it is capable of little active movement. It has undergone further degeneration in this genus than in related marine Isopods and is little more than a sheath for the maxillula *.

The *adductor* (*add.mx.*[2]) consists of three muscles originating close together on the medial edge of the sternal ala and divaricating to their insertion on the sclerite in the fossa of the appendage. The *abductor* (*abd.mx.*[2]) is a single muscle-band which originates on the posterior margin of the inner side of the genal fossa. It runs inwards and backwards looping round the lateral and medial pterygoid processes of the sternal ala of its side, and then passing forwards and downwards under the alar bar to its insertion in the maxilla about halfway up the lateral border of its supporting sclerite. This curious circuitous course seems to have been brought about by the backward migration of the maxillula and the endophragmal structures in connection with it in *Ligia*, which have come to lie on the outer side of the maxilla. The abductor, which would otherwise have an open route from the lateral wall of the cranium, is pushed back by the pterygoid processes until it comes to lie in an impression in the chitinous investment of these processes, as in a pulley surface (Pl. IV. fig. 17).

The effect of these muscles is to rock the maxilla on a fulcrum formed by the attachment of its basal sclerite to the alar bar.

The *Maxillipede* is capable, by its position, of downwards (and backwards) motion, but no muscle is provided for this movement, and it can only be effected by relaxing the large flexor muscles and thus allowing the appendage to drop. In practice the animal seems only to allow it to fall when it is using the endopod and basal endite like a scraping tongue, but it is usual in ill-preserved specimens in which the muscles are soft to find the appendage hanging loosely.

The *flexor* (*fl.mxp.*, Pl. IV. figs. 18 & 19) is a group of large and powerful muscles which have their origin on the alar bar in the concavity at the side of the median bar. They pass almost directly downwards, and are inserted on the inside of the basis and coxa by a broad insertion. It has been pointed out above that the basis is capable of moving laterally on the coxa. This action is brought about by two *abductors* (*abd.mxp.*, figs. 8 & 19) which originate on the maxillipedal sclerite at the point where the lateral margin of the coxa joins the bar and pass obliquely medially to be inserted on the inside of the maxillipede, one on the anterior (inner) face and one on the posterior (outer) face. There is no direct opponent of these muscles, and adduction is effected indirectly by the flexor.

* No light was thrown upon its action by removal of the maxillipedes of living specimens. These recovered from the operation and lived for some time, but could not be tempted to feed even on attractive soft food (such as soft roes of herring) without the aid of the maxillipede, and finally died of starvation.

## 8. *Comparative Terminology.*

| *Terms employed in this paper for the external features.* | *Usage of other authors.* |
|---|---|
| Antennary tubercle. | Many authors. |
| Clypeus. | Many authors. |
| Frontal lamina. | Mesepistome? (Dolf.), and many authors. |
| Frontal lobe. | Many authors. |
| Frontal line. | Linea frontalis marginalis. B. L. and many authors. |
| Gena (Entomol.). | Epimerienne (Dolf.). (Portion of pleural plate.) |
| Genal fossa (n. nov.). | —— |
| Genal groove (n. nov.). | Fossette pleurale (Dolf.). |
| Interocular line (n. nov.). | —— |
| Labrum. | Many authors. |
| Lateral lobe. | Many authors. |
| Lateral process (clypeus) (n. nov.). | Processus en corne (Dolf.). Clypeus ad latera lobatus (B. L.). |
| Marginal line. | Linea marginalis verticalis (in part) (B. L.). |
| Maxillipedal somite. | —— |
| Occipital groove (n. nov.). | Cervical groove of some authors. |
| Postfrons (n. nov.). | Prosepistome? (Dolf.). Epistome (in part.) (B. L.). |
| Postgena (Entomol.). | Episternal (Dolf.). (Portion of pleural plate.) |
| Postocular pit (n. nov.). | —— |
| Postfrons (n. nov.). | Prosepistome? (Dolf.). Epistome (in part) (B. L.). |
| Supra-antennal line (n. nov.). | Linea transversa epistomatis (B. L.). |
| Vertex. | Frons (B. L.). |

## Summary.

1. The external and internal features of the head of *Ligia oceanica* are described, and a terminology proposed for them and for similar structures in all terrestrial Isopods.

2. The 1st thoracic somite is shown to be distinctly demarcated from the head in this genus.

3. The "maxillosternal" framework and the endophragmal skeleton is described and its morphology discussed.

4. The mechanism and structure of the appendages of the head is described and compared with that of other Isopods.

5. The musculature of the head is described and its bearing on the form of the head and mechanism of the appendages is discussed.

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## *Abbreviations used in Text-figures and Plates.*

*abd.int.ant.* = abductor intermedius antennaris.
*abd.lat.ant.* = abductor lateralis antennaris.
*abd.mand.* = abductor mandibularis.
*abd.med.ant.* = abductor medius antennaris.
*abd.mx¹.ext.* = abductor maxillularis externis.
*abd.mx¹.int.* = abductor maxillularis internis.
*abd.mx².* = abductor maxillaris.
*abd.mxp.* = abductor maxillipedaris.
*add.inf.ant.* = adductor inferior antennaris.
*add.mand.* = adductor mandibularis.
*add.mx¹.ext.* = adductor maxillularis externis.
*add.mx¹.int.* = adductor maxillularis internis.
*add.mx².* = adductor maxillaris.
*add.obl.ant.* = adductor obliquus antennaris.
*al.bar.* = alar bar.
*ant¹.* = antennule.
*ant.tub.* = antennary tubercle.
*bas.* = basis.
*clp.* = clypeus.
*cx.* = coxa.
*dep.ant.* = depressor antennaris.
*dep.mx¹.* = depressor maxillularis.
*end¹.* = endite of præcoxa.
*end².* = endite of coxa.
*end³.* = endite of basis.
*ep.mxp.* = epipodite of maxillipede.
*fl.bas.mx¹.* = flexor basalis maxillularis.
*fl.mxp.* = flexor maxillipedaris.
*fos.gen.* = genal fossa.
*fr.* = postfrons.
*gen.* = gena.
*gr.gen.* = genal groove.
*inf.lat.pty.* = inferior lateral pterygoid process.
*lab.* = labrum.
*lam.fr.* = frontal lamina.
*lev.inf.ant.* = levator inferior antennaris.
*lev.sup.ant.* = levator superior antennaris.
*lin.ant.* = supra-antennal line.
*lin.fr.* = frontal line.
*lin.marg.* = marginal line.
*lin.oc.* = interocular line.
*mand.* = mandible.
*med.b.* = median bar.
*mx.b.* = maxillary bar.
*mx².* = maxilla.
*mx¹.bas.* = basal sclerite of maxillula.
*mx¹.ext.* = external endite of maxillula (of basis).
*mx¹.int.* = internal endite of maxillula (of præcoxa).
*mx¹.scl.* = maxillulary sclerite.
*mx².bas.* = basal sclerite of maxilla.
*mx².pty.* = maxillary pterygoid process.
*mx².scl.* = maxillary sclerite.
*mxp.scl.* = maxillipedal sclerite.
*occ.gr.* = occipital groove.
*p.cx.* = præcoxa.
*p.postoc.* = postocular pit.
*pf.* = profrons.
*pg.* = paragnath.
*postgen.* = postgena.
*pr.al.* = superior tendinous process of the sternal ala.
*pr.lat.* = lateral process of clypeus.
*pr.ph.* = pharyngeal process of the sternal ala.
*som.mxp.* = maxillipedal somite.
*sp.* = median spine of frontal lamina.
*st.al.* = sternal ala.
*ten.abd.* = tendon of abductor mandibularis.
*ten.add.* = tendon of adductor mandibularis.
*ter.al.* = tergal ala.
* = fissure between maxillipedal somite and cephalon where occipital groove passes to ventral surface of head.

## EXPLANATION OF THE PLATES.

All figures are of *Ligia oceanica*. The author wishes gratefully to acknowledge the assistance of Miss Lilian Russell, M.Sc., and Mr. Frank Forty in the preparation of Plates I. and II.

### Plate I.

Fig. 1. Front view of the head.
Fig. 2. Lateral view of the head.

### Plate II.

Fig. 3. Internal skeletal structures of the head as seen from behind (looking into the "foramen magnum").
Fig. 4. Internal skeletal structures of the head viewed from the dorsal surface. The whole of the dorsal surface of the head-capsule has been removed and the sternal ala of the left side has been cut away.

### Plate III.

Fig. 5. Right maxillula viewed from anterior (inner) aspect.
Fig. 6. Basal sclerite of maxillula with muscles and attachments viewed from behind.
Fig. 7. Left maxilla and attachments from posterior (outer) aspect. The nearer arthrodial membrane is shown by cross lines running obliquely upwards to the right, the farther by reverse lines.
Fig. 8. Left maxillipede viewed from posterior (outer) aspect.
Figs. 9, 10, & 11. Successive dissections of the muscles of the antenna. 9, viewed from above *in situ*; 10, the levators have been removed and the adductor obliquus turned aside. The dorsal faces of præcoxa, coxa, and basis have been cut away; 11, adductor inferior and obliquus and abductor lateralis removed, præcoxa and coxa further cut away. (See Plate IV. for fig. 11.)

### Plate IV.

Fig. 11. (For description see under Plate III. above.)
Fig. 12. Right maxillula from posterior (outer) aspect to show the muscles.
Fig. 13. Base of the inner (præcoxal) endite of same from posterior (outer) aspect to show muscles: detached from basal sclerite.
Fig. 14. Base of the same from medial aspect.
Fig. 15. The same from anterior (inner) aspect.
Fig. 16. Left maxilla from anterior (inner) aspect to show muscles (the abductor turns out of the plane of this figure).
Fig. 17. Structures of right latero-ventral corner of the head viewed from behind to show the course of the abductor maxillaris.
Fig. 18. Left maxillipede viewed from the medial aspect to show its muscles. The alar bar and maxillipedal sclerite have been cut through.
Fig. 19. The same viewed from the anterior (inner) aspect.

# 45. Contributions to the Development of the Pelvic Girdle: I.—The Pelvic Girdle in the Batrachian *Menopoma alleghaniense* Harlan. By James W. Low, B.Sc., F.Z.S., Department of Zoology, University of Bristol.

[Received March 9, 1926: Read April 27, 1926.]

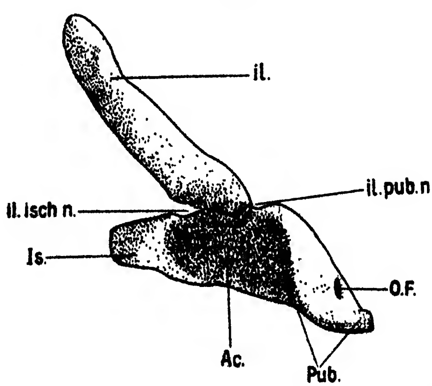
(Text-figures 1–4.)

The present paper consists of a description of three stages in the development of the pelvic girdle of *Menopoma*. The material consisted of embryos, 27 mm., 32·5 mm. and 38 mm. respectively, for which I am indebted to Professor F. H. Edgeworth and Dr. W. D. Henderson. Transverse sections (10 $\mu$) were cut of the hinder portions of these and reconstructions of the pelvic girdles made by the wax-plate method. The pelvic nerves of the 32·5 mm. and 38 mm. embryos, and in the latter case also the muscles having their origin or insertion in the pelvic region, were reconstructed.

## The Pelvic Girdle in the 27 mm. Embryo. (Text-fig. 1.)

At this stage the pelvic girdle consists of two distinct halves, each of which is composed of a stout ventral portion and an

Text-figure 1.




Drawing of model (× 100) of right half of pelvic girdle of 27 mm. embryo. Lateral aspect, scale ½ approx. The thin area of the cartilage is indicated thus ----.

upwardly directed slender process. These two cartilages are inclined to one another at an angle of about 105°, so that they form a wide V-shaped structure, lying close to the ventral body-wall.

Each half forms a definite mass of cartilage in which a dorsal iliac region, an antero-ventral pubic region, and a postero-ventral ischial region are roughly indicated, and the girdle will be described according to these regions. It should be noted, however, that there is no discontinuity in the cartilaginous mass and the regions are mainly based on comparisons with other forms. Each cartilage bears on its outer size, at about the middle of its length and below the point of origin of the iliac process, a shallow depression, the acetabulum, with which the femur articulates.

Fossa acetabuli:

The acetabulum consists of a shallow depression, facing ventrolaterally, on the outer side of each cartilaginous mass. It lies in the area of union of iliac, ischial and pubic regions, and, in my opinion, a portion of each of these takes part in the formation of the acetabular surface. The acetabulum is marked off from the pubic and ischial regions by fairly prominent ridges and less noticeably marked off dorsally, where the acetabular surface is continuous with the outer surface of the ilium. In its hinder part the acetabulum is indented by a deep notch, the acetabular portion of the large ilio-ischiadic notch which lies between the iliac process and the ischial region. This notch reaches inwards towards the centre of the acetabulum and from about this point the cartilage is thinned out in a line passing forwards and upwards to another (ilio-pubic) notch, probably marking the anterior limit of the iliac region.

Regio iliaca:

The iliac portion of the cartilage consists of a rather flattened prong-like process arising dorsal to the acetabulum and projecting obliquely upwards, backwards and outwards, with its anterior limit probably indicated by the thin region of the cartilage referred to above. The inner surface of this process is slightly concave from its attachment to its free posterior end, and the process rather oval in section. The outer surface curves gradually at its lower end into the acetabular surface. The anterior border is narrow and rounded, and slopes downwards from the free end to a wide shallow notch which separates it from the dorso-lateral border of the pubic region. The posterior border is broad and rounded and slopes downwards and forward, bounding the ilio-ischiadic notch dorsally, to the acetabular portion of that notch, where it is much thinner.

Regio ischiadica:

The ischial region consists of a mass of cartilage broad anteriorly, in the acetabular region, and tapering towards its caudal end. The acetabular portion is triangular in section, with the apex directed obliquely upwards. The dorsal surface is smooth with a slight ridge anteriorly, which passes obliquely forwards across the surface from the apex of the ilio-pubic notch to the

ventro-medial edge of the cartilage. The ventro-lateral surface is rounded and passes in front, laterally into the acetabular surface, from which it is separated by a slight ridge, and ventrally into the ventral surface of the pubic region. The dorso-lateral border is fairly broad and round, and extends from the ilio-ischiadic notch to the free posterior end. The ventro-medial border is rounded and continuous with the ventro-medial border of the pubic region.

Regio pubica:

The pubic region consists of a mass of cartilage lying in front of the acetabulum. It is somewhat triangular in transverse section, the apex being directed upwards. Passing forward from the acetabulum, the ventro-lateral angle is drawn out as a flattened wing-like projection forming a pubic plate, abruptly truncated in front.

The dorsal surface of the pubic portion is smooth and is continuous behind with the dorsal surfaces of the ischial and iliac regions, from which it is separated by a shallow groove, which probably indicates the hinder limit of the pubic region, lying in front of the ridge on the anterior end of the ischial region. The ventral surface, perforated near its centre by a small obturator foramen, is continuous with the ventral surface of the ischial region. The obturator foramen lies in a depression, and from it a shallow longitudinal groove runs forward to the anterior margin. The lateral surface consists of two aspects, an acetabular face and a pre-acetabular face, separated by a fairly prominent ridge bounding the acetabulum anteriorly. The acetabular face extends downwards from the notch separating iliac and pubic regions to the ventro-lateral margin of the acetabulum, forming part of the acetabular surface. The pre-acetabular face is triangular in area and slopes forward as far as the obturator foramen, which opens somewhat obliquely at its anterior edge, thus lying between the dorso-lateral margin and a wing-like expansion lying at right angles to the pre-acetabular face, in the same plane as the prolonged end of the dorso-lateral margin. The median border of the pubic region is rounded and is continuous behind with the median border of the ischial region. The ventro-lateral border forms an elbow at the lower edge of the ridge bounding the acetabulum and passes forward as the lateral border of the pubic plate. The anterior aspect forms a small, somewhat dumb-bell-shaped area.

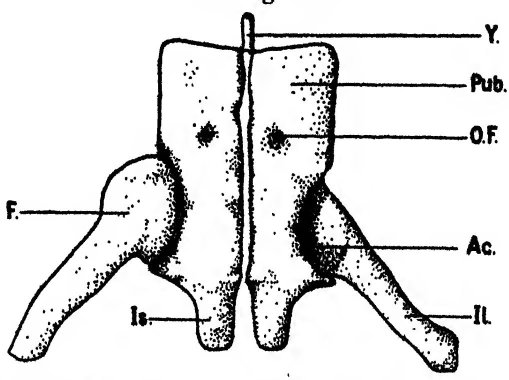
A slight aggregation of cells in the mid-ventral line, in front of the pubic region and slightly ventral to it, may indicate the beginning of the primordium of the ypsiloid cartilage.

The ventral surface of the pubo-ischium slopes upwards from the anterior border at an angle of about 30° to the vertebral axis. The dorso-lateral edge of the ischial region lies about parallel to that axis.

### The Pelvic Girdle in the 32·5 mm. Embryo. (Text-fig. 2.)

As compared with the 27 mm. stage, very considerable development has taken place. The length of the girdle is about twice that of the younger stage, largely due to the formation of flat pubic plates. The girdle still consists of two distinct halves, but the angle between them is reduced to about 90°. The acetabulum is more completely formed. The oblique groove on the dorsal surface of the pubic region, which probably indicated its hinder limit, has disappeared, so that the dorsal surfaces of pubic and ischial regions form a flat continuous surface. There is little, if any, trace of the ilio-pubic notch. Considerable changes have taken place in the ischial region, its post-acetabular portion being more plate-like and projecting backwards at a higher level than the ventral surface of the acetabular portion. The primordium of the ypsiloid cartilage has made its appearance in procartilage.

Text-figure 2.




Drawing of model (× 100) of pelvic girdle of 32·5 mm. embryo. Ventral aspect, scale ½ approx.

Fossa acetabuli:

The acetabulum has become deeper, faces more laterally, and is more definitely demarcated from the surrounding regions. The acetabular portion of the ilio-ischiadic notch is now filled up, the cartilage in the neighbourhood being greatly thickened, forming a fairly broad posterior ridge. This, together with a more ventral process of the ischial region, bounds the acetabulum posteriorly. The ridge is indented by a notch surrounding the head of the femur. Passing forward from the upper end of this notch is an oblique ridge which separates the outer surface of the ilium from the acetabular surface. In front of the anterior end of this ridge the acetabular surface passes dorsally into the dorso-lateral margin of the iliac and pubic regions. Anteriorly the acetabulum

is bounded by a ridge at the lateral edge of the acetabular face of the pubic region. This passes below into the elbow which forms the hind end of the lateral margin of the pubic plate. Below the acetabulum the ventro-lateral margin has become narrower and forms a slight rim, which is slightly concave from before backwards.

Regio iliaca:

The probable anterior limits of the iliac region are no longer distinguishable at this stage, but, in my opinion, a small part of the flat dorsal surface of the whole ventral portion of the cartilage is probably formed by the iliac region, the prong-like process of which expands somewhat as it merges in the ventral cartilage above and behind the acetabulum. The iliac process has become somewhat flattened towards its free posterior end. Its upper border is consequently narrower at that end, but becomes broader more anteriorly and is continuous with the dorso-lateral border of the pubic region, there being little, if any, trace of the notch present in the earlier stage. The posterior border at its lower end passes into a fairly broad posterior surface, separated from the acetabulum by the ridge mentioned above.

Regio ischiadica:

This region has become much more distinctly differentiated into an acetabular portion, roughly triangular in transverse section, and a small quadrangular plate-like portion, flattened dorso ventrally, projecting backwards. These portions are separated ventrally by a pronounced transverse ridge.

The ventral surface of the acetabular portion is continuous in front with the ventral surface of the pubic region. Behind the transverse ridge it curves sharply upwards and passes into the ventral surface of the ischial plate, which lies parallel to the vertebral axis. The ridge is prolonged laterally into a process bounding the post-acetabular notch below. The dorsal surface of the ischial region is continuous anteriorly with the dorsal surface of the pubic region and dorsally with that of the iliac region. The medial borders of the ischial plates of either side are more widely separated than are the corresponding borders of the acetabular portions, which are closely approximated in the mid-ventral line.

Regio pubica:

The pubic region of the girdle has greatly increased by the formation of two flat pubic plates in front of the acetabular region. The pre-acetabular face of the lateral aspect of the earlier stage has now become antero-dorsal, forming a triangular face between the dorsal surface of the acetabular portion of this region and that of the pubic plate. The pubic plate is flattened dorso-ventrally, quadrangular in outline, and is thicker near the rounded lateral border, from which it slopes gradually inwards to

the narrower medial border. The anterior margin is flat and curves slightly backwards at the antero-median angle. At this point the two pubic plates are in procartilaginous continuity with a small cylindrical mass of procartilage lying in the mid-ventral line and slightly below the level of the ventral surface of the pubic region. This is the primordium of the ypsiloid cartilage.

### The Pelvic Girdle in the 38 mm. Embryo. (Text-figs. 3 & 4.)

The girdle has only slightly increased in size as compared with the 32·5 mm. stage. Its total length shows a slight increase, but the relative proportions are somewhat different. The dorsal surfaces of the cartilages of either side are now inclined to one another at an angle of about 60°, and the ventro-medial borders are more closely approximated in the mid-ventral line, especially in the acetabular region, where the ventral surfaces bulge downwards. The pubic plates have increased slightly in length and are oblong instead of quadrangular, and the obturator foramina are relatively larger. The thickness of the cartilage in the acetabular region has increased slightly. The iliac processes are longer, and both the length and breadth of the ischial plates have increased. The ilio-ischiadic notch is wider. The acetabulum has not increased in size, but is more clearly separated off from the surrounding surfaces.

Fossa acetabuli:

The cartilage covering the back of the acetabulum is thicker and above forms a broad ridge or lateral surface of the iliac and pubic regions overhanging the acetabulum. Anteriorly the cartilage has also become thicker, so as to obliterate the elbow formed by the hind end of the lateral border of the pubic plate in the earlier stage. Posteriorly the lateral process of the ventral ridge of the ischial region has become more prominent. The small post-acetabular notch is still present. Below the acetabulum the ventro-lateral border of the pubo-ischium forms a slightly more prominent rim.

Regio iliaca:

The iliac process is relatively longer than in the 32·5 mm. stage, but the relationships of this region are practically the same as in that stage. The ridge bounding the anterior part of the ilio-ischiadic notch has grown out somewhat, so that the posterior aspect is narrower. Laterally this surface slopes forwards to the ridge which bounds the acetabulum and has now become more prominent, as has also the ridge across the outer surface of the lower end of the iliac process.

Regio ischiadica:

This region has become drawn out posteriorly into two flat plates. These approximate more closely in the mid-ventral line

than in the 32·5 mm. embryo, and the posterior border of each is slightly convex. The dorsal surface of the ischial region is continuous anteriorly with the dorsal surface of the pubic region. On the ventral surface the transverse ridge has been obliterated, only the lateral portion of this remaining as a prominent process bounding the acetabulum behind and, together with the more dorsal ridge of the iliac region, forming a wide post-acetabular notch, in which the head of the femur lies.

Regio pubica:

The main alteration in the pubic region is the greater development of the pubic plate, which is now a flat oblong structure with its long axis longitudinal. The antero-dorsal surface in the region of the obturator foramen is less marked, and the dorso-lateral margin of the acetabular region passes more gradually into the dorsal surface of the pubic plate. The two pubic regions bulge ventrally towards the middle line in the acetabular region, and their ventro-medial borders are very closely approximated at that point. By thickening of the cartilage, the elbow at the hind end of the lateral border of the pubic plate has been obliterated, this border passing more gradually into the ventral part of the acetabular surface. Anteriorly the antero-medial angles of the pubic plates are continuous with flattened procartilaginous extensions, which merge with the cylindrical axis of the ypsiloid procartilage. This axis lies in the mid-ventral line and slightly ventral to the level of the pubic plates. Passing forwards the ypsiloid procartilage is at first nearly cylindrical in transverse section, but expands into two lateral wing-like projections, which are widest anteriorly. The anterior border is slightly convex.

## The Pelvic Muscles in the 38 mm. Embryo. (Text-figs. 3 & 4.)

The muscles related to the pelvic girdle were reconstructed in the model of the girdle of the 38 mm. embryo and are described below. The muscles are as far as possible named with regard to their origins and insertions, except in the case of well-established names about which little doubt exists as to their homologues in other Vertebrates. The synonyms used by other authors are given in the table on pages 920 & 921.

(A) The muscles passing backwards from the anterior end of the body which are inserted in the pelvic region are:—

M. rectus abdominis (pubo-thoracicus):

This consists of two narrow bands of muscle lying on either side of, and close to, the linea alba. Near the anterior pubic region each band is differentiated into two portions—a ventral portion, the fibres of which are inserted into the anterior border of the pubic plate, and a dorsal portion, whose fibres are inserted as a M. ypsiloideus posterior (Whipple, 15) into the stem of the

| *Terminology used in this paper.* | OSAWA, 1901. | HOFFMANN, 1873-78. | DE MAN, 1873. |
|---|---|---|---|
| M. rectus abdominis (pubo-thoracicus). | rectus abdominis. | pubo-thoracicus. | — |
| M. obliquus externus (costo-abdominalis externus). | obliquus externus. | costo-abdominalis externus (obliquus externus). | — |
| M. obliquus internus (costo-abdominalis internus). | obliquus internus. | costo-abdominalis internus (obliquus internus). | — |
| M. ischio-caudalis . . ..... ... . | ischio-caudalis. | ischio-caudalis. | — |
| M. caudali-pubo-ischio-tibialis ... | caudali-pubo-ischiadicus. | caudali-pubo-ischio-tibialis. | caudali-pubo-ischio-tibialis. |
| M. caudo-femoralis ... . ....... .... | caudo-femoralis. | caudali-femoralis. | caudali-femoralis. |
| M. pubo-ischio-tibialis ........... | pubo-ischio-tibialis. | pubo-ischio-tibialis. | pubo-ischio-tibialis. |
| M. ischio-flexorius ....... ........ | ischio-flexorius. | ischio-flexorius. | ischio-flexorius. |
| M. pubo-ischio-femoralis externus. | pubo-ischio-femoralis externus. | pubo-ischio-femoralis externus. | pubo-ischio-femoralis externus. |
| M. ischio-femoralis, $\alpha$ & $\beta$ ....... | ischio-femoralis. | ischio-femoralis. | ischio-femoralis. |
| M. pubo-ischio-femoralis internus. | Part of caput pubicum of extensor femoris biceps. | pubo-ischio-femoralis internus. | Pubo-ischio-femoralis internus. |
| M. pubo-extensorius .. .. ........ | Part of caput pubicum of M. extensor femoris biceps. | apparently included in M. pubo-ischio-femoralis internus. | — |
| M. ilio-extensorius ........... ...... | ilio-extensorius. | ilio-extensorius (in part). | ilio-tibialis. |
| M. ilio-femoralis (anterior and posterior). | ilio-femoralis. | ilio-femoralis. | ilio-femoralis. |
| M. ilio-femoro-fibularis′ ........ | Ilio-fibularis. | Ilio-femoro-fibularis. | Ilio-fibularis. |
| M. ilio-femoro-fibularis″ ...... | Femoro-fibularis. | | — |

| HUMPHRY, 1872. | MIVART, 1869. | DUGÈS, 1834. | MECKEL, 1824. | STANNIUS, 1846. |
|---|---|---|---|---|
| rectus abdominis. | rectus. | pubio - sous - sternal. | Gerader Bauchmuskel. | — |
| obliquus externus. | external oblique. | oblique externe ou costo-abdominal. | Aeusserer schiefer Bauchmuskel. | — |
| obliquus internus. | internal oblique. | oblique interne ou vertébro-abdominal. | Innerer schiefer Bauchmuskel. | — |
| ischio-caudal. | ischio-caudal. | — | — | — |
| caudo-crural. | semimembranosus. | coccy-sous-fémoral. | subcaudalis. | subcaudalis. |
| caudo-femoralis. | femoro-caudal. | coccy-sous-fémoral. | pyriformis. | pyriformis. |
| Superficial stratum of plantar muscles of thigh (in part) or gracilis. | gracilis. | Sous-ischio-tibial. | Zweiter Beuger. | Flexores adducentes. |
| Superficial stratum of plantar muscles of thigh (in part) or caudo-pedal-caudo-crural. | Semitendinosus. | — | Langer, starker Beuger. | Flexores adducentes. |
| Middle part of the deeper stratum of plantar muscles of thigh. | Adductor. | Ex-pelvi-fémoral. | Nach aussen Zieher. | Obturatorius and Adductor ischiadicus. |
| Hinder ischio-femoral part of deeper stratum of thigh muscles. | ischio - femoral (not described in *Menopoma*). | — | Gemellus. | Quadratus femoris. Gemellus. |
| Anterior or supra-pubic portion of the deeper stratum of plantar muscles of thigh or pectineus. | iliacus. | Intra-pelvi-fémoral. | Pectineus. | Pectineus. |
| Inner sector of superficial stratum of dorsal muscles of thigh or rectus femoris internus. | rectus femoris. | — | — | — |
| Middle sector of superficial stratum of dorsal muscles of thigh or gluteo-rectus. | gluteus maximus. | — | Starker strecker. | Steckmuskelmasse des Unterschenkels. |
| Ileo-femoral stratum of dorsal muscles of thigh. | Gluteus medius and Gluteus minimus. | Ileo-rotulien. | — | Glutæus. |
| Outer sector of superficial stratum of dorsal muscles of thigh. | Ileo-peroneal. | Ileo-péronien. | Wadenbein beuger. | Abductor fibularis primus. |
| Femoro-fibularis (?) | Biceps. | Femoro-péronien. | — | Abductor fibularis secundus. |

developing ypsiloid cartilage. This latter portion corresponds to the M. pyramidalis of Hoffmann.

M. [illegible] ius

This contin[illegible] a ventral aponeurosis and be[illegible] anterior part of the pubic p[illegible] of the origin of the M. pubo-isc[illegible]

M. obliquus internus (costo-abdominalis internus):

This muscle is partly attached [illegible] the dorsal [illegible] of the ilium, just above the origin of the M. ilio-extensorius.

(B) The muscles passing forwards from the tail which are inserted in the pelvic region are.—

M. ischio-caudalis:

This is the most median of the sub caudal muscles. It is a broad thin plate of muscle lying obliquely to the vertical plane, and is inserted into the postero-lateral angle of the ischial plate.

Innervation: An ischio-caudal branch from the sciatic plexus.

M. caudali-pubo-ischio-tibialis:

This is a small muscle which passes forwards between the adjacent sides of the M. ischio-caudalis and M. caudo-femoralis, and is inserted into the posterior edge of the M. pubo-ischio-tibialis a short way after the latter muscle has left the ischial region. Some fibres also pass to the posterior edge of the M. ischio flexorius.

Innervation: N. pudendus.

M. caudo-femoralis:

This is a fairly large muscle, round in section, which lies lateral to the M. ischio-caudalis. It tapers anteriorly into a long tendon, which is inserted into the femur below the trochanter and dorsal to part of the insertion of the M. pubo-ischio-femoralis externus.

Innervation: N. pudendus.

(C) The ventral muscles of the thigh are;—

M. pubo-ischio-tibialis:

This is a very large triangular sheet of muscle which arises from an aponeurosis in the mid-ventral line, along the whole line of approximation of the halves of the pubo-ischium. It runs with converging fibres laterally and distally, to be inserted into the tibia.

Innervation: A branch of the N. tibialis communis and N. obturatorius.

M. ischio-flexorius:

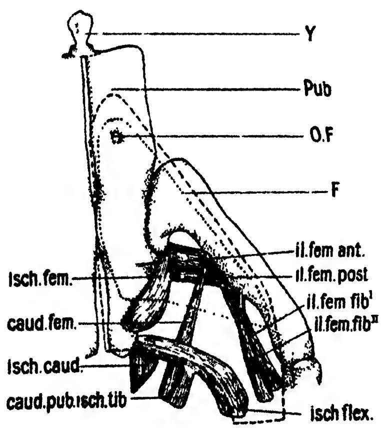
This muscle arises from the postero-lateral angle of the ischial plate [illegible] ...tion of the M. ischio-caudalis, and passe[illegible] knee.

Innervation: Not determined. According to Osawa supplied by the same nerve as the previous muscle.

M. pubo-ischio-femoralis externus:

This is a thick triangular muscle. It arises from the ventral surface of the pubo-ischium near its median border. The origin reaches from about half-way along the pubic plate anteriorly to

Text-figure 3.




Drawing of left half of model (× 150) of the pelvic girdle of 38 mm. embryo. Ventral aspect, scale ⅓ approx. The position of the M. pubo-ischio-tibialis is indicated by - - - - - - - - - and that of the M pubo-ischio-femoralis externus by ......... .... (The M. caudali-pubo-ischio-tibialis is inserted partly into the M. ischio-flexorius, as shown, and partly into the more ventral M. pubo-ischio-tibialis.)

about half-way along the ischial plate posteriorly. It is entirely covered by the M. pubo-ischio-tibialis. It is inserted into the femur partly just below the attachment of the M. caudo-femoralis and partly just below and distal to the origin of the femoro-fibular head of the M. ilio-femoro-fibularis down to the tibial condyle.

Innervation: N. obturatorius and a small branch of the N. tibialis communis.

M. ischio-femoralis:

At this stage I find that the muscle thus named in the adult consists of two intimately associated muscles:—

(α) A dorsal, more or less cylindrical, muscle, arising from the lateral border of the ischial plate, anterior to the origin of the M. ischio-flexorius, and passing forwards to be inserted on the head of the femur; and

(β) a ventral, more irregularly shaped, muscle, intimately associated with the above near its origin, which arises from the ventral surface of the ischial plate, immediately below the origin of α, and passes forwards to be inserted in the capsule of the hip-joint.

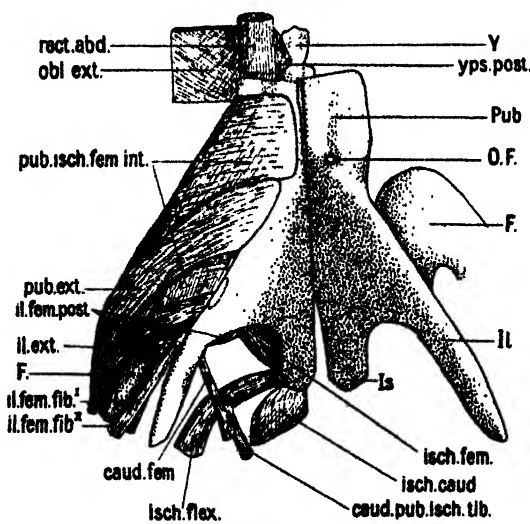
Innervation: A small branch from the sciatic plexus.

(D) The dorsal muscles of the thigh are:—

M. pubo-ischio-femoralis internus:

This muscle arises from the middle line along the whole dorsal surface of the pubic region and the dorso-lateral border of the

Text-figure 4.




Drawing of model (× 150) of pelvic girdle of 38 mm. embryo. Dorsal aspect, scale ⅓ approx.

ilium. It passes over the lateral margin of the girdle and the dorsal side of the hip-joint, where it bends at an obtuse angle, and passes downwards, expanding over the dorsal side of the femur, into the lower two-thirds of which it is inserted.

Innervation: N. femoralis and a twig from the N. obturatorius.

M. pubo-extensorius:

This is a strap-shaped muscle which arises from the dorso-lateral border of the acetabular portion of the pubic region, immediately above and closely associated with part of the origin of the M. pubo-ischio-femoralis internus, and passes downwards over that muscle to be inserted in an aponeurosis on the tibial side of the knee.

Innervation: N. femoralis.

M. ilio-extensorius:

This is a strap shaped muscle which arises from the outer surface of the iliac process immediately behind the M. pubo-ischio-femoralis internus and passes downwards to be inserted by a flat tendon in the lower leg. It is separated from the knee by the origin of the dorsal muscles of the lower leg.

Innervation: N. femoralis.

M. ilio-femoralis:

This consists of two very closely associated muscles, which may be named M. ilio-femoralis anterior and posterior respectively. The anterior muscle arises from the iliac region just above and behind the acetabulum. It is covered by the M. ilio-extensorius and is inserted into the peroneal side of the femur. The posterior muscle is larger and arises from the posterior surface of the iliac region, immediately opposite the origin of the anterior muscle, and is inserted into the femur near and dorsal to that muscle.

Innervation: N. peroneus.

M. ilio-femoro-fibularis:

This is a two-headed muscle. The ilio-fibular head is a long slender muscle which arises from the outer surface of the ilium immediately below and in very close connection with the origin of the M. ilio-extensorius. It passes down to be inserted about the middle of the peroneal side of the fibula. The femoro-fibular head is also a slender muscle which arises from the femur below and distal to the insertion of the M. caudo-femoralis and passes downwards beside the ilio-fibular head, with which it becomes intimately associated at its insertion.

Innervation: A branch from the N. tibialis.

## Discussion.

The chief account of the Myology of *Menopoma alleghaniense* is given by Mivart (**7**), while Osawa (**9**), Humphry (**3**), and to some extent Schmidt, Goddard and van der Hoeven (**12**) deal with the musculature of *Cryptobranchus japonicus*. A general account of the muscles of Urodeles is also given by Hoffmann (**2**) and de Man (**5**). Many authors refer to the possible homologies of the various muscles with those of man or higher Vertebrates

Such references are omitted as far as possible in this paper, the question of homologies being reserved for future discussion.

The subcaudal muscles as they pass from behind forward towards the pelvic region divide into three, M. ischio-caudalis, M. caudo-femoralis and M. caudali-pubo-ischio-tibialis.

The two first-named muscles are similarly named by most workers, but there is diversity of opinion with regard to the third, here named M. caudali-pubo-ischio-tibialis. According to Osawa, this muscle, which he calls M. caudali-pubo-ischiadicus, in *Cryptobranchus* "verbindet sich mit dem hinteren Rand des M. pubo-ischio-tibialis resp. ischio-flexorius sehnig." Hoffmann states that the muscle in question joins the M. pubo-ischio-tibialis. Humphry, describing the same species, names this muscle the caudo-crural and states that it joins "the superficial stratum of the plantar muscles of the thigh almost at right angles." He further states that a bundle of fibres of the hinder part of the muscular mass thus described, and which he considers appears to correspond to the semitendinosus of man, although he does not describe it as a separate muscle, "joins a similar bundle from the caudo-crural and they together form the caudo-pedal." This agrees with Mivart's description for *Menopoma*, but in this case the posterior bundle of fibres is described as a separate muscle, the semitendinosus, arising from the posterior-external angle of the ischium and passing down the leg. The semimembranosus, which is Mivart's name for the M. caudali-pubo-ischio-tibialis, "is inserted into the posterior edge of the semitendinosus a little after the latter muscle has left the ischium." He considers that it may perhaps be a second head of the semitendinosus. The reconstruction made of the muscles in the 38 mm. embryo shows that the M. caudali-pubo-ischio-tibialis is inserted partly into the posterior edge of the M. pubo-ischio-tibialis and partly into the posterior edge of the M. ischio-flexorius.

The most superficial of the ventral muscles of the thigh is the large triangular M. pubo-ischio-tibialis which covers the others, with the exception of the M. ischio-flexorius, which lies behind and slightly beneath it. Removal of this muscle exposes the M. pubo-ischio-femoralis externus, while still deeper the M. ischio-femoralis passes from the ischial plate to the head of the femur.

The M. ischio-femoralis is described by Osawa in *Cryptobranchus japonicus* as a small muscle arising from the lateral border of the ischium and inserted into the capsule of the hip-joint and the adjacent part of the femur. It is not referred to by Mivart as occurring in *Menopoma*. In the 38 mm. embryo I find that there are, in this position, two intimately associated muscles, as described above (p. 924).

The superficial muscles of the dorsal aspect of the thigh consists of:—

(A) A large muscle (here called M. pubo-ischio-femoralis internus) arising from the dorsal surface of the pubic region and the dorso-lateral border of the ilium, and inserted into the lower portion of the femur;

(B) a strap-like muscle (M. pubo-extensorius) lying above this, arising from the dorso-lateral border of the acetabular portion of the pubic region, and inserted in an aponeurosis on the tibial side of the knee; and

(C) another strap-like muscle (M. ilio-extensorius) which arises from the outer surface of the iliac process behind the M. pubo-ischio-femoralis internus and passes downwards over the knee to be inserted in the lower leg.

Mivart (7) and Humphry (3) describe these as separate muscles with origins and insertions as described (pp. 924 & 925).

The names given by these authors are:—

| Muscle. | Mivart. | Humphry. |
|---|---|---|
| A...... | Iliacus. | Pectineus. |
| B...... | Rectus femoris. | Rectus femoris internus. |
| C...... | Gluteus maximus. | "Gluteo-rectus." |

Osawa (9) describes all these muscles together as constituting a M. extensor femoris biceps, which, he states, is a two-headed muscle, one head (caput pubicum) arising from the whole inner surface of the pars pubica of the pubo-ischium, passing over the margin of the pubic region and the dorsal side of the hip-joint capsule, and passing downwards to the dorsal side of the femur, the other head (caput iliacum), which is equivalent to C (M. ilio-extensorius), taking its origin from the anterior border of the medial half of the ilium and likewise passing downward over the hip-joint. He further describes these two heads as having a common insertion on the whole dorsal surface of the femur down to the condyle. B is apparently included with A in the caput pubicum. Hoffmann and de Man describe A as a M. pubo-ischio-femoralis internus and C as a separate M. ilio-extensorius, with origin and insertion as described (p. 925), and not as passing to a common insertion with the M. pubo-ischio-femoralis internus. de Man considers that Mivart's separation of this muscle (C) into two portions is artificial, but the portions described by Mivart as separate muscles correspond to C and B, the latter apparently being included with A by these workers. Examination of the reconstruction of the muscles of the 38 mm. embryo and of serial transverse sections confirms Mivart and Humphry's description that B (M. pubo-extensorius) is a separate muscle passing down over A (M. pubo-ischio-femoralis internus) to be inserted in an aponeurosis on the tibial side of the knee.

The M. ilio-femoralis is described by most authors as a single muscle. In the adult *Menopoma*, Mivart describes two closely associated muscles, Gluteus medius and Gluteus minimus respectively. My observations confirm this description of the two muscles, for which the names M. ilio-femoralis anterior and posterior are suggested (p. 925).

As regards the M. ilio-femoro-fibularis, this is in some cases described as two separate muscles, in others as two heads of one muscle; there is general agreement that the two components

seem to represent the long and short heads of the Biceps femoris of higher animals, and they are consequently described under one name.

*The Nerves of the Pelvic Region.*

The nerves supplying the pelvic region and the hind limb are derived from four spinal nerves. As only the hinder portion of the embryo was sectioned, it is impossible to state which spinal nerves are concerned, but these correspond to the N. præsacrales III, II, and I and the N. sacralis of Osawa (9). The terminology used by Osawa is adopted here.

The pelvic nerves form plexi anterior and posterior to the iliac process. The anterior or lumbar plexus is formed by the N. præsacrales III and II. This gives two main branches:—

N. obturatorius: Runs forwards to the inner side of the pubic region. It penetrates the M. pubo-ischio-femoralis internus, to which it gives a twig, and passes through the obturator foramen and enters the M. pubo-ischio-tibialis. Just at its origin it gives a ramus hypogastricus which supplies the skin in that region.

N. femoralis: Passes over the dorso-lateral border of the pubo-ischium just in front of the iliac process. The main trunk (ramus longus, Osawa) penetrates the M. pubo-ischio-femoralis internus and passes distally close to the inner side of the femur. A small branch (ramus brevis, Osawa) supplies the M. ilio-extensorius.

The larger posterior or sciatic plexus is formed by the N. præsacrales II and I and the small N. sacralis. This sciatic plexus lies behind and below the iliac process, between the M. ischio-flexorius and M. caudo-femoralis. Its main branches are:—

N. peroneus: Arises from the outer side of the plexus rather dorsally and just after leaving the plexus gives a twig to the M. ilio-femoralis and to the M. ilio-femoro-fibularis (ilio-femoral head).

N. tibialis communis: This is the largest nerve of the hind limb. From its origin it is divided into two trunks, which are separated from one another by the M. caudo-femoralis and the femoro-fibular head of the M. ilio-femoro-fibularis. These two trunks unite just above the knee. A smaller collateral trunk runs beside the more ventral of the two main trunks and joins with it at the knee.

N. pubo-ischio-tibialis: A small nerve which arises from the antero-ventral region of the plexus and enters the M. pubo-ischio-tibialis.

N. pudendus: A small nerve which supplies the M. caudali-pubo-ischio-tibialis and M. caudo-femoralis.

N. ischio-caudalis: Arises from the N. sacralis and supplies the M. caudo-femoralis and M. ischio-caudalis.

I wish to express my best thanks to Dr. W. D. Henderson for much helpful advice during the progress of the work.

### *Abbreviations used in Text-figures.*

*Ac.* Acetabulum. *caud.fem.* M. caudo-femoralis. *caud.pub.isch.tib.* M. caudali-pubo-ischio-tibialis. *F.* Femur. *Il.* Iliac region. *il.fem.ant.* M. ilio-femoralis anterior. *il.fem.post.* M. ilio-femoralis posterior. *il.ext.* M. ilio-extensorius. *il.fem.fib.'* Ilio-fibular head of M. ilio-femoro-fibularis. *il.fem.fib.''* Femoro-fibular head of M. ilio-femoro-fibularis. *il.pub.n.* Ilio-pubic notch. *il.isch.n.* Ilio-ischiadic notch. *Is.* Ischial region. *isch.fem.* M. ischio-femoralis. *isch.flex.* M. ischio-flexorius. *obl.ext.* M. obliquus externus. *O.F.* Obturator-foramen. *Pub.* Pubic region. *pub.ext.* M. pubo-extensorius. *pub.isch.fem.int.* M. pubo-ischio-femoralis internus. *rect.abd.* M. rectus abdominis. *Y.* Ypsiloid pro-cartilage. *yps.post.* M. ypsiloideus posterior.

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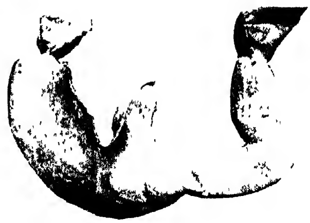

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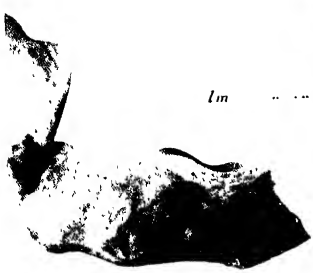

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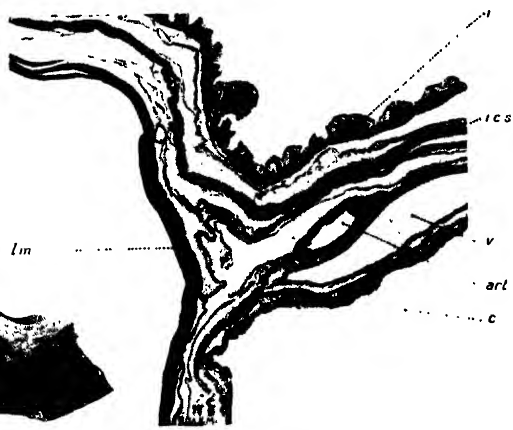



4

THE ILEO-CAECAL REGION OF
*TUPINAMBIS TEGUEXIN*

# 46. The Ileo-Cæcal Region in the Reptilia.—I. The Ileo-Cæcal Region of *Tupinambis teguexin*. By John Beattie, M.B., Ch.B., M.Sc., C.M.Z.S.

[Received March 23, 1926: Read April 13, 1926.]

(Plate I.; Text-figures 1, 2.)

The specimen on which this note is based was collected by Professor J. P. Hill on the Percy Sladen Expedition to Brazil in 1913. The animal was eviscerated after capture and the ileo-cæcal region preserved in alcohol. A small segment was embedded and sectioned. I desire to thank Professor Hill for putting the material at my disposal.

Lönnberg in 1902 made a series of observations on the gut of the reptiles with reference to the influence of diet on the structure of the gut tube. He was able to show that the proximal colon in the Reptilia became enlarged to form diverticula to allow of the proper digestion of the cellulose-containing foods on which some of the animals fed. The complexity of the proximal part of the large bowel became greater with a more complete herbivorous diet. *Tupinambis* is interesting in that it is only partly herbivorous, although in the specimen which is described here the stomach contained dark brown seeds alone when the animal was captured.

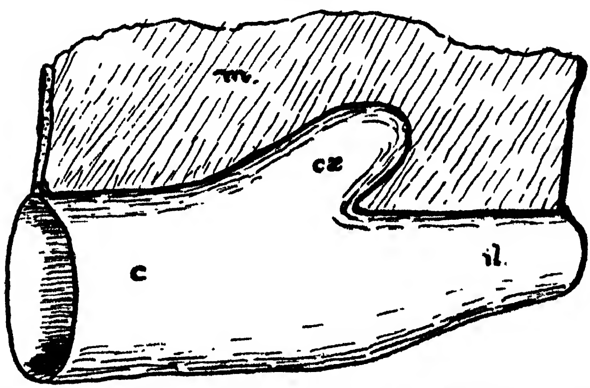
The structure of the cæcum and proximal colon in *Tupinambis* is intermediate between the very simple arrangement seen in the Amphisbæna and the complex arrangement of the Iguana and its closely-allied form *Metopoceros cornutus*. In all three the ileum at its termination is pouched out to form a conical sac with the base at the ileo-cæcal diaphragm (which contains within it the ileo-cæcal sphincter). This ileal expansion may be a post-mortem change, but as it is constant in most of the animals which have been examined it is possible that it is a normal feature.

The ileum is covered with large villi which do not appear to have any regular arrangement, but are scattered over the whole of the surface of the ileum and closely packed together. They cover the ileal surface of the ileo-cæcal diaphragm, and there they are of low elevation and terminate abruptly at the free margin of the orifice.

The diaphragm in the *Tupinambis* is an annular band of tissue with a central opening. This central arrangement of the opening is found in most of the Lizards, but in the Iguana Tuberculata it is eccentric and the annular band is replaced by a semi-lunar fold of tissue. The interest of the diaphragm lies

in the structure of the muscle tissue lying within it. The section shown in fig. 4, Pl. I. demonstrates the fact that the circular muscle coat of the bowel alone enters into the composition of the sphincter. The outer longitudinal coat passes over the sphincter region in a continuous sheet. The circular muscle tissue is in two distinct layers which do not fuse together except at the free margin of the diaphragm. Between the two layers of muscle a large artery and vein run in the connective tissue and are seen to supply the sphincter muscle and the other structures of the diaphragm. This arrangement is closely analogous to the condition seen in the developing mammal, especially in the early stages of Man. There the developing ileo-cæcal sphincter muscle

Text-figure 1.




The internal appearance of the ileo-cæcal region of *Amphisbæna alba* to show a lateral cæcum which at its base is lying in close apposition to the mesentery.
*c.* colon ; *cæ.* cæcum ; *il.* ileum.

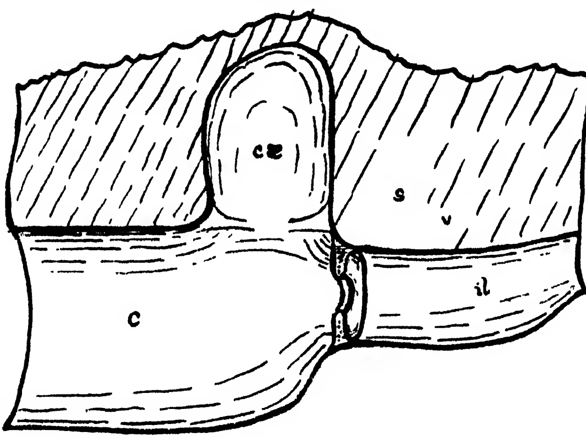
is differentiated only from that layer of the mesoblastic coat of the intestine which comes to form at a later date the muscle cells of the circular muscle coat. The developing sphincter in Man, although it cannot be divided into two layers in the almost diagrammatic manner which is seen in the *Tupinambis*, is nevertheless split into two divisions to a lesser degree by a small blood-vessel in the same position as that in the *Tupinambis*.

The proximal colon in this animal shows a well-marked diverticulum from the mesenteric border, which penetrates between the two layers of the mesentery and is entirely covered with peritoneum. This condition would be quite inexplicable unless the arrangement of the part in *Metopoceros* is examined. In this animal the cæcum is a distinct diverticulum from the left side of the colon, and as it enlarges dorsally it comes to lie along the left surface of the mesentery and adheres to it. This

cæcum may illustrate a stage in the development of a cæcum in *Tupinambis*. The cæcum in this latter animal may have originated as a lateral cæcum, but with enlargement it has come to fuse so completely with the mesentery as to appear that it is enclosed within the mesentery. So far there is no evidence of a direct nature to justify this view, but it is hoped to examine some of the embryonic stages of this animal as they become available to establish this point.

The large bowel throughout its whole extent is quite free of villi, and shows only a small number of concentric elevations round the wall which consist of mucous tissue only. These

Text-figure 2.




The ileo-cæcal region of *Tupinambis tequexin* laid open along the plane of mesenteric attachment to show the position of the sphincteric ring or curtain between the ileum and large bowel. The cæcum is completely enclosed within the two folds of the mesentery of the gut.

*cæ.* cæcum; *c.* colon; *s.* sphincteric ring and valvular opening; *il.* ileum.

elevations are similar to the valvulæ conniventes in the upper intestine in the mammals and are probably similar in function. In the Iguana and in *Metopoceros* these "valvulæ" reach a high development, and the food-material is thus retained in a series of chambers where no doubt it is acted upon by the bacterial flora and the cellulose digested as much as possible.

It is hoped at a later date to make some further studies on this region in the other Lizards and the Amphibia, but as material is usually in a state which does not allow of histological methods, progress must be slow.

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## EXPLANATION OF THE PLATE.

Fig. 1. The ileo-cæcal region of *Tupinambis teguexin* laid open to show the sphincter ring and the cæcum lying in the mesenteric border of the gut.

Fig. 2. Obverse view of Fig. 1, to show the line of mesenteric attachment. Note how the cæcum is completely intra-mesenteric.

Fig. 3. *Amphisbæna alba.* The cæcum is lateral in its origin and not mesenteric as in *Tupinambis.* The photograph does not indicate the attachment of the base of the cæcum to the mesentery.

Fig. 4. *Tupinambis teguexin.* A section through the gut at right angles to the plane of the sphincteric ring. *i.* mucous membrane of ileum. *i.e.s.* the circular muscle of the sphincter embedded in the sphincteric ring. *v.art.* vessels in the sphincteric ring. *l.m.* longitudinal muscle of the intestine. *c.* colon.

# 47. Notes on the Habits of certain Families of the Order Marsupialia. By A. S. Le Souef, C.M.Z.S.

[Received May 7, 1926: Read June 1, 1926.]

Owing to the great physical difference that exists between Marsupials and the other orders of mammals, one would expect to find that their general habits and dispositions were not in accordance with those generally found in the higher animals. This seems to be the case. for a careful study of this group as represented in Australia indicates that they have a more primitive organisation in their herd groups and a distinctly lower sense of life-preservation.

In the birth of the young we find a striking instance of the apparent lack of that maternal care and affection that is so strongly manifest in other animals, as the mother is seemingly unaware of the babies' existence. As the young of Marsupials are born in such a primitive state, the fœtus of the great Grey Kangaroo being only one and a quarter inches in length at birth, one would expect to find that the dam took the greatest care of the helpless offspring, and transferred it to the pouch. Such, however, is not the case, as several observations of the birth of Kangaroos * and one of the American Opossum † show that the doe apparently does not take any interest in the new arrival, and the fœtus has, in spite of its unformed state, to make its own way to the pouch and attach itself to the nipple The female at this time sits in an upright position, with her tail coming forward between her legs and appears to be only concerned with cleaning the extruded fluid and blood from her fur. At a later stage, when the youngster is furred and able to take some interest in life, observations on Kangaroos and Wallabies show that the mother frequently licks and caresses her baby, while a female Pouched Mouse (*Sminthopsis murina*) has been seen to show great bravery and devotion in rescuing her young from an exposed position.

The great majority of the marsupials live singly, possibly the only exceptions being some of the larger Kangaroos and Tree-Kangaroos. Fairly large herds of the Great Grey (*Macropus giganteus*) and the Red (*M. rufus*) are not uncommon where the animals are numerous. These herds do not seem to have any organisation, in that they are not apparently under the leadership of a large male, nor do we notice any separation of the sexes, either according to age or at different times of the year.

* Proc. Phil. Soc. Queensland, vol. iii. 1881, p. 1; 'Western Mail,' Perth, Western Australia, Jan. 9, 1913.

† 'Anatomical Record,' vol. xix. 1920, p. 251.

When attacked the members of a herd do not necessarily make off in one direction, and often become scattered. Individual old male Kangaroos are brave and determined fighters if brought to bay. They will then back up against a tree or a rock, and attempt to rip and tear any enemy that comes within reach.

Many animals get amusement from friendly combats. In the Kangaroos these contests, which take place only between males, have been developed to a higher degree than is usual among other animals. The game takes the form of a sparring and kicking contest, divided into definite rounds, between which the animals rest.

The vocal sounds made by the terrestrial diprotodonts are very primitive in character, and consist of only a single coughing note in the Kangaroo and Wallaby group *, and a husky growling in the Rat-Kangaroos and Wombats. This note never varies in expressing pleasure, anger, pain, or distress. There appears to be no call-note, but alarm is signalled by thumping the hind feet on the ground, a trait that is shared by some rodents.

Some of the arboreal members of the diprotodonts (Phalangeridæ) have a much more highly-developed voice. The Australian Opossums (*Trichosurus* and *Pseudochirus*) and the Koala (*Phascolarctus*) can each make two distinct and very different sounds. The call-note of the Koala closely resembles the grating wood-sawing cry of the Leopard, and in addition it has a plaintive wailing cry that is only made when the animal is injured. The most striking call-note of any of the Marsupials is given by the greater Flying Phalanger, and to a lesser extent by other members of this group. This call is quite distinct, as far as I know, from that of any other mammal. It consists of a series of modulated shrieking sounds, starting loud and full and running down the scale to a mere gurgle. The Cuscus and smaller members of the Phalanger group have not been heard to utter any sound.

All the Phalangeridæ are particularly quiet and docile and lack any aggressiveness, and in this respect they show a low sense of life-preservation.

The disposition of the Australian Carnivorous Marsupials is in marked contrast to that usually found in flesh-eaters. Carnivorous animals generally are elusive, aggressive, and when cornered quick to defend themselves from capture. The Australian Carnivorous Marsupials are quite the reverse of this, for they have an extraordinarily quiet and trusting disposition. Some members of the family Dasyuridæ can be handled as soon as caught, while live Phascogales have actually been picked up in the bush. Two instances will serve to illustrate this peculiar disposition. Two specimens of the Crested-tailed Phascogale (*Dasycercus cristicauda*), which had been caught on the Nullar-

* [In the Zoological Gardens here, a Kangaroo, being anæsthetised for a slight operation, gave a prolonged, undulating cry recalling that of the Thylacine.—EDITOR P. Z. S.]

bor Plain, South Australia, escaped and took refuge among a number of packing-cases in a lumber-room; when a baited trap was placed near one of the animals it went straight in and the other one took a bait from my hand and allowed itself to be picked up. On another occasion a farmer on the Arthur River, Tasmania, came across a Spotted-tailed Dasyure (*Dasyurus maculatus*) in broad daylight feeding on the carcase of a Wallaby: he made a hit at it with an axe that he was carrying, but missed the animal. The Dasyure jumped clear, but did not run away, and presently returned to the carcase as if nothing had happened, although the man was standing beside it with uplifted weapon. This Dasyure can, nevertheless, put up a hard fight and give a very good account of itself if attacked by a dog or exasperated by being caught in a trap.

The voice of all the Carnivorous Marsupials is very primitive in character. The Marsupial Wolf or Thylacine can only express itself by a coughing sound, and the Tasmanian Devil * (*Sarcophilus*) makes a slow whining noise, while the smaller Dasyures do not appear to make any other sound than a slight hiss. These animals seem to have no distinctive call.

To sum up this brief review, we find that there is a singular lack of maternal interest in the young at time of birth. That the organisation so often present in herds of Herbivores is absent in mobs of Kangaroos. That the voice of all Australian terrestrial Marsupials is very primitive in character, while most of the arboreal species have a well-developed call, which differs from their note of distress, and, finally, we can note the very quiet and non-aggressive nature of Australian members of the order, which gives them a relatively low sense of life-preservation. This factor would make them quite unfitted to withstand competition from the higher mammals.

* [That is not our experience here; the Thylacine often utters a prolonged, and very loud, undulating cry, and Tasmanian devils, especially at night, are very noisy animals.—Ed. P. Z. S.]

## EXHIBITIONS AND NOTICES.

### June 1st, 1926.

Sir JOHN BLAND-SUTTON, Bt., F.R.C.S., Vice-President, in the Chair.

The SECRETARY read the following Report on the Additions to the Society's Menagerie during the month of April, 1926:—

The registered additions to the Society's Menagerie during the month of April were 302 in number. Of these 76 were acquired by presentation, 7 were deposited, 198 were purchased, 8 were received in exchange, and 13 were born in the Menagerie.

The following may be specially mentioned:—

1 Grevy's Zebra (*Equus grevyi*) ♂, from Kenya, purchased on April 8th.

1 Chimpanzee (*Anthropopithecus troglodytes*) ♀, presented by T. D. Maxwell on April 21st.

1 Chimpanzee (*Anthropopithecus troglodytes*) ♂, presented by Arthur Haserick, F.Z.S., on April 22nd.

4 Prairie Wolves (*Canis latrans*), born in the Menagerie on April 6th.

2 Kea Parrots (*Nestor notabilis*), from New Zealand, purchased on April 22nd.

3 Indian Coursers (*Cursorius coromandelicus*), and 2 Red-wattled Lapwings (*Sarcogrammus indicus*), from India, both new to the collection, received in exchange on April 30th.

1 Dollo's Lung-Fish (*Protopterus dolloi*), from the Belgian Congo, new to the collection, received in exchange on April 29th.

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Dr. FRANK CHAPMAN exhibited, and made remarks upon, a series of lantern-slides illustrating the Bird and Mammalian Life on the Barro Colorado Island, Panama.

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### June 15th, 1926.

Prof. E. W. MACBRIDE, F.R.S., Vice-President, in the Chair.

The SECRETARY read the following Report on the Additions to the Society's Menagerie during the month of May, 1926:—

The registered additions to the Society's Menagerie during the month of May were 146 in number. Of these 68 were acquired by presentation, 8 were deposited, 60 were purchased, 1 was received in exchange, and 9 were born in the Menagerie.

The following may be specially mentioned:—

A collection from Gambia, consisting of an African Civet, a Senegal Zorilla, Gambian Gerbille, two Ashy-headed Gulls, a Royal Python, and other reptiles, presented by H.E. Captain Sir C. H. Armitage, C.M.G., D.S.O., F.Z.S., on May 23rd.

2 Giant Rats (*Cricetomys gambianus*), from Kenya Colony, presented by Captain A. T. A. Ritchie, M.C., F.Z.S., on May 30th.

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The SECRETARY communicated the following notes by T. D. MAXWELL, Esq., on a young female Chimpanzee presented to the Society:—

"On April 23, 1925 she was acquired by an ex-boy of mine in Mamfe-Ossidinge, Cameroons (about 100 miles N.W. of Duala). She was then 'about the size of a Rat: had little hair: no teeth: was unable to walk or crawl but lay on her back and whimpered incessantly.' I gather she was then 2 or 3 weeks old, and put her birthday down as the 1st of April, 1925. The boy and his wife brought her up on the bottle. At the end of July she started to crawl, and then he noticed she was cutting a few teeth."

"She came to me on the 26th of December, 1925, she weighed 10 lbs 6 oz. She was a mere baby, and still cutting her teeth. She was very active but quite unable to climb. During February she began to do so, and is now an expert. On February 10th, she weighed 11 lbs. 2 oz.; on March 10th, 13 lbs.; on April 10th, 15 lbs. Mentally and physically she developed with amazing speed. She is an extremely intelligent little animal—far more so already than Pat (aged 4) and Okon (2) ever became. She has a weakness for hugging a woolly ball, or a bit of cloth or towel. I always indulged her in this. She also is very fond of her teething ring (a black bracelet), and her native rattle."

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Major S. S. FLOWER, O.B.E., F.Z.S., exhibited, and made remarks upon, models of a White Elephant from Siam.

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Dr. R. J. TILLYARD, F.R.S., C.M.Z.S., gave an account of "Some new Orders of Fossil Insects," illustrated by a remarkable series of lantern-slides.

Prof. HENRY FAIRFIELD OSBORN, C.M.Z.S., President of the American Museum of Natural History, who was present, said that he would like to felicitate Dr. Tillyard upon his recent researches, and at the same time to congratulate the Society upon the progress it had made since his last visit to London some fifteen years ago.

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['Proceedings,' 1926, Part II. (pp. [illegible] and Index), was published on July 15, 1926.]

# 48. A Synopsis of the Rays of the Family Rhinobatidæ, with a Revision of the Genus *Rhinobatus*. By J. R. Norman, F.Z.S.

(Offered for publication by permission of the Trustees of the British Museum.)

[Received May 22, 1926: Read October 19, 1926.]

(Text-figures 1–30.)

The family Rhinobatidæ as defined below corresponds with the subfamily Rhinobatinæ of Regan's classification of the Selachian fishes *, and includes the families Rhinobatidæ and Discobatidæ of Garman †.

I have to thank the Trustees of the Australian Museum for sending me an example of *Aptychotrema banksii*; Mrs. R. Bisbee, of the Zoological Department of the University of Liverpool, for specimens of *Rhinobatus halavi*; and Dr. L. Vinciguerra for the loan of examples of *R. rhinobatus* and *R. cemiculus* from the collections of the Genoa Museum. I am greatly indebted to Mr. C. Tate Regan, F.R.S., for much help and advice, and to Major W. P. C. Tenison, D.S.O., who has kindly prepared the illustrations accompanying this paper.

## Rhinobatidæ.

Batoid Rays with the præorbital cartilages articulated to the propterygia; two rather large, subequal dorsal fins, the anterior of which is situated at some distance from the extremity of the tail; pelvics not notched; caudal fin present; basalia of dorsal fin in small number (two only supporting the radials of the fin); radials rather numerous, simple, short or of moderate length, not nearly extending to the free edge of the fin; snout not armed with teeth.

Nine genera from tropical and temperate seas.

### Synopsis of the Genera.

I. Rostral cartilage extending to extremity of snout, or nearly.
- A. Origin of first dorsal above, in advance of, or immediately behind pelvics, which are situated well behind the pectorals; a well-developed subcaudal lobe; pectorals not extending forward beyond level of mouth.
  - 1. Snout broad, rounded; mouth deeply undulated; length of nostril less than width of internarial space; no spiracular folds .. .................. ...... . 1. Rhina.

* Proc. Zool. Soc. 1906, p. 754.
† Mem. Mus. Comp. Zool. xxxvi. 1913, pp. 266, 287.

2. Snout long, narrow, pointed; mouth not deeply undulated; length of nostril greater than width of internarial space; two spiracular folds ............ 2. RHYNCHOBATUS.

B. Origin of first dorsal well behind pelvics, which are situated close to the pectorals; no distinct subcaudal lobe; pectorals extending forward beyond level of mouth, but well separated anteriorly.

1. Snout pointed, sometimes short and obtuse; pectorals not extending forward to level of extremity of snout; anterior part of tail with a single median series of spines or tubercles; no spines on anterior edges of pectorals.

a. Anterior nasal valves not united to form a quadrangular flap.

* Nostrils oblique, or occasionally nearly transverse; inward extension of anterior nasal valve terminating on or crossing anterior margin of nostril (text-fig. 1 C): one or two spiracular folds ........ . ........ ........ ........ 3. RHINOBATUS

** Nostrils nearly transverse; inward extension of anterior nasal valve crossing inner angle of nostril (text-figs. 1 D, 1 E).

† Snout long, acutely pointed; anterior nasal valve covering only a small portion of inner part of nostril (text-fig. 1 D); spines on the back and shoulders small .............. 4. APTYCHOTREMA.

†† Snout short, obtusely pointed; anterior nasal valve expanded, almost entirely covering inner part of nostril (text-fig. 1 E); spines on the back and shoulders very prominent . 5. ZAPTERYX.

b. Anterior nasal valves united to form a quadrangular flap (text-fig. 1 F); snout short, obtusely pointed .................................... 6. TRYGONORHINA.

2. Snout very short, rounded; pectorals extending forward to level of extremity of snout; anterior part of tail with a longitudinal series of spines on either side of the median series; series of spines on anterior edges of pectorals ........................ 7. PLATYRHINOIDIS.

II. Rostral cartilage reduced, not reaching extremity of snout; snout broad and rounded; pectorals extending forward to end of snout, narrowly separated anteriorly.

A. Nostril not connected with mouth by a groove; anterior nasal valve not covering inner part of nostril (text-fig. 1 H); back with several series of spines in addition to the median and scapular series ........... 8. ZANOBATUS.

B. Nostril connected with mouth by a groove; anterior nasal valve expanded, partly covering inner part of nostril (text-fig. 1 I); only the median and scapular series of spines present ............ ..... ........ ...... . 9. PLATYRHINA.

## 1. RHINA.

*Rhina* * Bloch, Schneider, Syst. Ichth. p. 352 (1801); Müller & Henle, Plagiost. p. 110 (1841).

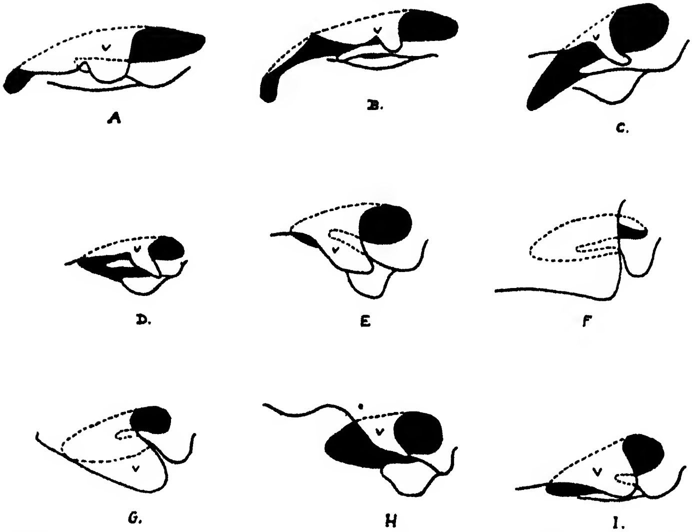
*Rhamphobatis* Gill, Ann. Lyceum Nat. Hist. N.Y. vii. 1862, p. 408; Garman, Mem. Mus. Comp. Zool. xxxvi. 1913, p. 267.

*Rhynchobatus* (part.) Günther, Cat. Fish. viii. p. 440 (1870).

A single species from the Indo-Pacific.

* *Rhina* Klein (type *Squalus squatina* Linn.) is not elegible according to the rules of the International Commission of Zoological Nomenclature. Klein's genera were reprinted in an anonymous dictionary ("Neuer Schauplatz") in 1776, and by Walbaum (Artedi Pisc.) in 1792. This does not, however, involve the acceptance of these names.

Text-figure 1.




Diagrams illustrating the form of the nostril in:—A. *Rhina ancylostoma.* B. *Rhynchobatus djiddensis.* C. *Rhinobatus rhinobatus.* D. *Aptychotrema bougainvillii.* E. *Zapteryx brevirostris.* F. *Trygonorhina fasciata.* G. *Platyrhinoidis triseriatus.* H. *Zanobatus schœnleinii.* I. *Platyrhina sinensis.* V.=anterior nasal valve.

1. Rhina ancylostoma.

*Rhina ancylostoma* Bloch, Schneider, Syst. Ichth. p. 352, pl. lxxii. (1801); Müller & Henle, Plagiost. p. 110 (1841); Jordan & Fowler, Proc. U.S. Nat. Mus. xxvi. 1903, p. 643.

*Rhina anchylostomus* Bleeker, Verh. Bat. Gen. xxiv. 1852, Plag. p. 56.

*Rhina cyclostomus* Swainson, Nat. Hist. ii. p. 322 (1839).

*Rhamphobatis ancylostomus* Duméril, Elasmobr. p. 482 (1865); Annandale, Mem. Ind. Mus. ii. 1909, p. 10, pl. 5. fig. 5; Garman, Mem. Mus. Comp. Zool. xxxvi. 1913, p. 267.

*Rhynchobatus ancylostomus* Günther, Cat. Fish. viii. p. 440 (1870); Day, Fish. India, p. 730, pl. cxciii. fig. 3 (1878).

*Hab.* East Africa and the Red Sea, through the Indian Ocean and Archipelago to Australia and Japan.

In the British Museum ten specimens, 420 to 1900 mm. in total length.

2. Rhynchobatus.

*Rhynchobatus* Müller & Henle, Monatsber. Ak. Berlin, 1837, p. 116; Plagiost. p. 111 (1841); Garman, Mem. Mus. Comp. Zool. xxxvi. 1913, p. 268.

*Rhynchobatus* (part.) Günther, Cat. Fish. viii. p. 440 (1870).

Two species.

1. RHYNCHOBATUS DJIDDENSIS.

*Raja djiddensis* Forskal, Descr. Anim. p. 18 (1775).

*Rhinobatus lævis* Bloch, Schneider, Syst. Ichth. p. 354, pl. lxxi. (1801); Schlegel, Faun. Japon. p. 306, pl. cxxxix. (1850).

*Rhinobatus djidsensis* Bloch, Schneider, *t. c.* p. 356.

*Rhinobatus djeddensis* Rüppell, Fische Roth. Meers, p. 54, pl. 14. fig 1 (1828); Annandale, Mem. Ind. Mus. ii. 1909, p. 12.

? *Rhinobatus duhamelii* Blainville, Faun. Franç., Poissons, p. 48 (1830).

*Rhynchobatus lævis* Müller & Henle, Monatsber. Ak. Berlin, 1837, p. 116; Plagiost. p. 111 (1841); Duméril, Elasmobr. p. 483 (1865).

*Rhinobatus ruepellii* Swainson, Nat. Hist. ii. p. 185, fig. 24 (1838).

*Rhynchobatus dji(e)ddensis* Cantor, J. Asiat. Soc. Bengal, xviii. 1850, p. 1394; Günther, Cat. Fish. viii. p. 441 (1870); Day, Fish. India, p. 730, pl. cxcii. fig. 1 (1878); Jordan & Fowler, Proc. U.S. Nat. Mus. xxvi. 1903, p. 644; Günther, Fische Südsee, ix. p. 491 (1910); Garman, Mem. Mus. Comp. Zool. xxxvi. 1913, p. 268, pl. 65. fig. 1; Barnard, Ann. S. African Mus. xxi. 1925, p. 58, pl. iii. fig. 6.

*Rhinobatus jaram* Montrouzier, Ann. Sci. Phys. Nat. Agric. Lyon, ser. 2, viii. 1856, p. 498.

Mouth undulated. Anterior nasal valve extending beyond the middle of the length of the nostril. Origin of first dorsal above base of pelvics. No spines on rostral cartilage.

*Hab.* East Africa and the Red Sea to the Pacific.

In the British Museum several specimens, 100 to 2000 mm. in total length.

2. RHYNCHOBATUS ATLANTICUS.

*Rhynchobatus atlanticus* Regan, Ann. Mag. Nat. Hist. ser. 8, xv. 1915, p. 124.

Mouth straight, except for a median prominence in the lower jaw fitting an emargination in the upper. Anterior nasal valve ending at the middle of the length of the nostril. Origin of first dorsal behind base of pelvics. Spines stronger and fewer than in *R. djiddensis*; a series on each side of rostral cartilage.

*Hab.* Off Lagos, West Africa, 10 to 35 fms.

In the British Museum a single specimen (♂), 700 mm. in total length, type of the species.

3. RHINOBATUS.

*Rhinobatos* Linck, Mag. Neuste Phys. Nat. vi. (3) 1790, p. 32.

*Rhinobatus* Walbaum (*ex* Klein), Artedi Ichth. (3) ed. 2 p. 581 (1792); Garman, Mem. Mus. Comp. Zool. xxxvi. 1913, p. 269.

*Leiobatus* Rafinesque, Caratteri, p. 16 (1810).

*Rhinobatus* (part.) Müller & Henle, Plagiost. p. 113; Günther, Cat. Fish. viii. p. 441 (1870).

*Syrrhina* (part.) Müller & Henle, Plagiost. p. 113 (1841).

*Glaucostegus* Bonaparte, Cat. Metod. Pesci Europ. p. 14 (1846).

Twenty-seven species *.

### Synopsis of the Species.

*Mediterranean, West African, and Indo-Pacific Species.*

I. Anterior nasal valve not or scarcely extending inwards on to internarial space. (*Rhinobatus.*)

A. Length of nostril twice or nearly twice in width of mouth, about equal to that of internarial space.

1. Snout long, narrow, its præoral length $2\frac{3}{5}$ to $3\frac{1}{4}$ times width of mouth; rostral ridges approximated for the greater part of their length . . . .. ...... 1. *granulatus*.

2. Snout short, broad, its præoral length $1\frac{5}{8}$ times width of mouth; rostral ridges more or less separated throughout their length .. . .... .... . . . 2. *obtusus*.

B. Length of nostril less than twice in width of mouth, greater than that of internarial space.

1. Snout expanded at the tip; length of nostril $1\frac{1}{4}$ in width of mouth, nearly twice that of internarial space ... .. ..... . . ..... 3. *thouiniana*.

2. Snout not expanded at the tip.

*a*. Length of nostril nearly equal to width of mouth, $2\frac{1}{4}$ to $2\frac{2}{5}$ times that of internarial space 4. *armatus*.

*b*. Length of nostril $1\frac{1}{3}$ to $1\frac{2}{3}$ in width of mouth, $1\frac{1}{3}$ to $1\frac{7}{8}$ times that of internarial space.

* Origin of first dorsal a distance behind base of pelvics about equal to that between the two dorsals; præorbital length of snout 3 to $3\frac{1}{3}$ times distance between spiracles.

† Distance from tip of snout to anterior edge of eye rather less than that from posterior edge of eye to axil of pectoral (in adults); a single pair of spines on each shoulder arranged thus : 5. *cemiculus*.

†† Distance from tip of snout to anterior edge of eye about equal to that from posteror edge of eye to axil of pectoral; two spines on each shoulder arranged thus • • . .... . ...... .... 6. *rasus*.

** Origin of first dorsal a distance behind base of pelvics $1\frac{2}{3}$ to nearly twice that between the two dorsals; præorbital length of snout $2\frac{2}{3}$ to 3 times distance between spiracles.. ..... .. ........ 7. *halavi*.

* The following species (without diagnoses) listed by Blainville (Bull. Soc. Sci. Philom. Paris, 1816, p. 121) are indeterminable:—*Rhinobatus russellianus*, *R. coromandelicus*, *R. fasciatus?*, *R. bifurcata*, *R. lævissimus*; *Leiobatus cruciatus*, *L. sloani*, *L. britannicus*.

I have been unable to identify *Rhinobatus dumerili* Castelnau (Proc. Zool. Soc. Victoria, ii. 1873, p. 148), from Western Australia. This may be a species of *Zapteryx*.

II. Anterior nasal valve extending inwards to some extent on to internarial space. (*Leiobatus.*)

A. Anterior nasal valve not extending inwards much beyond level of inner edge of nostril, not nearly reaching that of opposite side.

1. Snout rather long, its præorbital length $2\frac{3}{5}$ to $3\frac{1}{4}$ times distance between spiracles, its præoral length $3\frac{1}{3}$ to $3\frac{2}{3}$ times width of mouth; base of first dorsal 3 to $3\frac{3}{5}$ in distance between dorsals.

*a.* Rostral ridges widely separated throughout their length; length of nostril $1\frac{3}{5}$ times width of internarial space; some blunt tubercles in the median line of the back .............. .......... . ....... .. ... 8. *holcorhynchus.*

*b.* Rostral ridges approximated or narrowly separated anteriorly; length of nostril $1\frac{1}{5}$ to $1\frac{1}{2}$ times width of internarial space; tubercles in the median line of the back very small or rudimentary.

* Rostral ridges more or less separated throughout their length, approximated only at extremity of snout; horizontal distance from outer edge of nostril to lateral margin of snout a little less than length of nostril .. ..... . .... .... ........ 9. *formosensis.*

** Rostral ridges more or less approximated in anterior $\frac{2}{3}$ of their length; horizontal distance from outer edge of nostril to lateral margin of snout greater than length of nostril .. ........... 10. *schlegelii.*

2. Snout shorter, its præorbital length $2\frac{1}{3}$ to nearly 3 times distance between spiracles, its præoral length $2\frac{1}{3}$ to 3 times width of mouth; base of first dorsal less than 3 times in distance between dorsals.

*a.* Præoral length of snout $2\frac{1}{3}$ to $2\frac{1}{2}$ times width of mouth; both spiracular folds well developed.

* Space between rostral ridges rather narrow; base of first dorsal $2\frac{1}{4}$ to $2\frac{3}{4}$ in distance between dorsals; a series of spines in the median line of the back ................ ............................ 11. *annandalei.*

** Space between rostral ridges broader; base of first dorsal $2\frac{3}{5}$ in distance between dorsals; a series of minute tubercles in the median line of the back ........... ...................... .............. 12. *lionotus.*

*b.* Præoral length of snout $2\frac{2}{3}$ to 3 times width of mouth; inner spiracular fold small or rudimentary.

* Rostral ridges rather broad, narrowly separated anteriorly; origin of first dorsal a distance behind base of pelvics $1\frac{1}{5}$ to $1\frac{1}{4}$ times that between the two dorsals; tubercles in median line of back rudimentary; back pale brownish, with groups of small dark spots.. ................. 13. *hynnicephalus.*

** Rostral ridges narrow, widely separated throughout their length: origin of first dorsal a distance behind base of pelvics a little less than that between the two dorsals; a series of small spines in the median line of the back; coloration of back uniform ........................................ 14. *rhinobatus.*

B. Anterior nasal valve extending inwards well beyond level of inner edge of nostril, nearly meeting that of opposite side.

1. Both spiracular folds developed; præoral length of snout $2\frac{1}{2}$ to $3\frac{1}{2}$ times width of mouth.

*a.* Præorbital length of snout 2 to $2\frac{3}{5}$ times distance between spiracles; length of nostril about equal to width of internarial space.

* Præoral length of snout $2\frac{3}{4}$ to 3 times width of mouth; horizontal distance from outer edge of nostril to lateral margin of snout 3 to $3\frac{2}{3}$ times in præoral length of snout; back with dark annular ocelli . . . . . . . . . . . . . . . 15. *annulatus.*

** Præoral length of snout $2\frac{1}{4}$ to $2\frac{2}{3}$ times width of mouth; horizontal distance from outer edge of nostril to lateral margin of snout $2\frac{1}{2}$ to $2\frac{2}{3}$ in præoral length of snout: snout and pectoral fins with pale bluish-grey spots and blotches . . . . . . . 16. *leucospilus.*

*b.* Præorbital length of snout nearly 3 times distance between spiracles; length of nostril $1\frac{1}{2}$ times width of internarial space.

* Width of mouth 3 in præoral length of snout, $7\frac{1}{2}$ in distance from tip of snout to anterior edge of vent; horizontal distance from outer edge of nostril to lateral margin of snout more than 4 in præoral length of snout; coloration uniform . 17. *zanzibarensis.*

** Width of mouth $3\frac{1}{2}$ in præoral length of snout, more than 8 in distance from tip of snout to anterior edge of vent; horizontal distance from outer edge of nostril to lateral margin of snout $3\frac{2}{3}$ in præoral length of snout; back with numerous bluish-grey ocelli 18. *ocellatus.*

2. Only the outer spiracular fold developed; præoral length of snout $2\frac{1}{4}$ to $2\frac{2}{3}$ times width of mouth 19. *blochii.*

## *American Species.*

Anterior nasal valve not, or only slightly extending inwards on to internarial space.

I. Two spiracular folds.

A. Upper surface freckled with numerous small white spots; rostral ridges narrowly separated, almost parallel . . . . . . . . . . . 20. *lentiginosus.*

B. Upper surface uniformly coloured, or with larger white or bluish-grey spots and blotches.

1. Rostral ridges widely separated throughout their length.

*a.* Rostral ridges rather broad; back with regularly arranged slate-coloured blotches . . 21. *glaucostigma.*

*b.* Rostral ridges narrow; back without blotches . . 22. *leucorhynchus.*

2. Rostral ridges more or less approximated, at least anteriorly.

*a.* Back with regularly arranged smallish white spots; præorbital length of snout nearly 3 times distance between spiracles . . . . . . . . . . . . . . 23. *stellio.*

*b.* Back uniformly coloured, or with irregularly scattered spots.

* Præorbital length of snout $2\frac{1}{3}$ to $2\frac{1}{2}$ times distance between spiracles; rostral ridges more or less approximated for anterior half of their length . 24. *productus.*

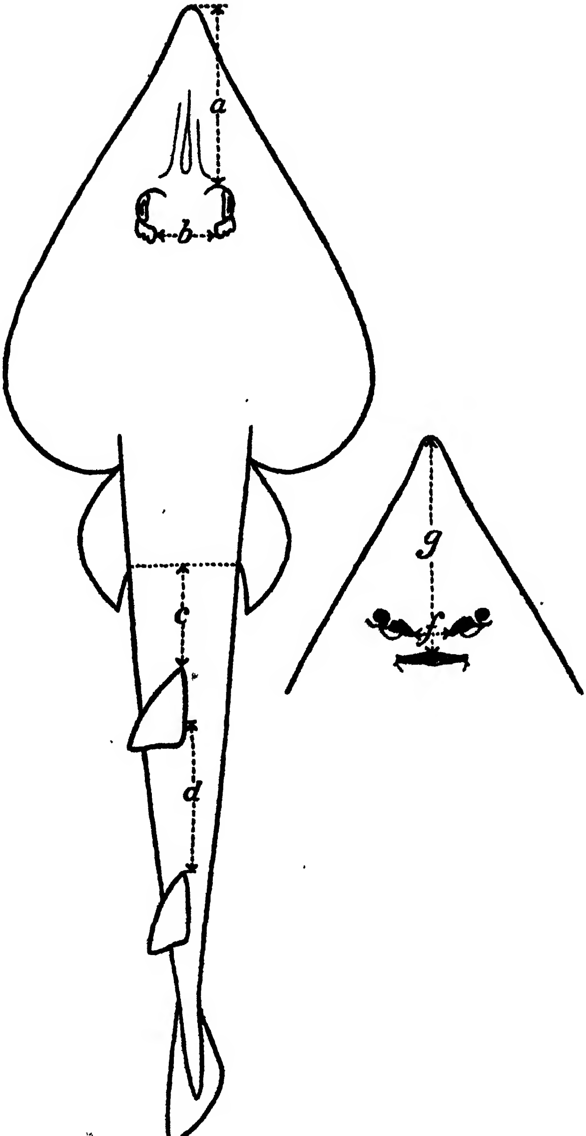
** Præorbital length of snout $2\frac{2}{3}$ to 3 times distance between spiracles; rostral ridges more or less approximated for rather more than half their length.

† Length of nostril $1\frac{1}{3}$ to nearly twice in width of mouth, a little greater than that of internarial space; interorbital space rather concave . . . . . . . . 25. *percellens.*

†† Length of nostril $1\frac{1}{3}$ in width of mouth, nearly $1\frac{1}{2}$ times that of internarial space; interorbital space flat . . . . . . . . . . . . . . . . . 26. *horkelii.*

II. Spiracle with a single rudimentary fold . . . . . . . . . 27. *planiceps.*

Text-figure 2.




Diagrammatic figure of a specimen of *Rhinobatus*, to illustrate certain measurements used in the descriptions of the species.

*a*=preorbital length of snout. *b*=distance between spiracles. *c*=distance between origin of first dorsal and base of pelvics. *d*=distance between the two dorsals. *f*=internarial width. *g*=præoral length of snout.

1. RHINOBATUS GRANULATUS.

*Rhinobatus granulatus* Cuvier, Règne Anim. ed. 2, ii. p. 396 (1829); Annandale, Mem. Ind. Mus. ii. 1909, p. 14; Garman, Mem. Mus. Comp. Zool. xxxvi. 1913, p. 272.

*Rhinobatus* (*Rhinobatus*) *granulatus* Müller & Henle, Plagiost. p. 117, pl. 38 (1841); Duméril, Elasmobr. p. 493 (1865); Bleeker, Verh. Bat. Gen. xxv. 1853, Bengal, p. 82.

? *Rhinobatus* (*Rhinobatus*) *philippi* Müller & Henle, *t. c.* p. 119, pl. 39 (1841).

*Rhinobatus tuberculatus* (Cuvier) Bleeker, *t. c.* p. 82.

*Rhinobatus granulatus* (part.) Günther, Cat. Fish. viii. p. 443 (1870); Day, Fish. India, p. 732, pl. cxcii. fig. 2 (1878).

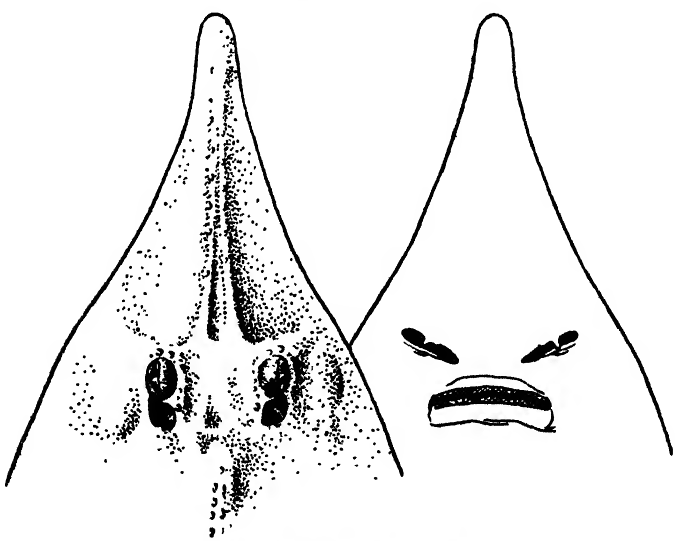
*Rhinobatus spinosus* Günther, *t. c.* p. 518 (1870).

*Rhinobatus thouini* Day, *t. c.* p. 732, pl. cxc. fig. 4 (1878).

*Rhinobatus acutus* Garman, Bull. Mus. Comp. Zool. li. 1908, p. 253; Mem. Mus. Comp. Zool. xxxvi. 1913, p. 273, pl. 17 *b*. figs. 1 2.

Snout long, acute, the margins straight or rather concave; its præorbital length $3\frac{1}{4}$ to $3\frac{2}{3}$ times the distance between the spiracles,

Text-figure 3.



*Rhinobatus granulatus.* (× ½.)

and its præoral length $2\frac{2}{3}$ to $3\frac{1}{4}$ times width of mouth. Rostral ridges narrow, closely approximated for more than half their length, diverging a little posteriorly. Diameter of eye 9 (young) to 14 in præorbital length of snout, that of eye + spiracle about $1\frac{1}{3}$ in distance between spiracles. Outer fold of spiracle feebly

developed, inner rudimentary or absent. Nostrils rather short, nearly transverse, nearly twice in width of mouth, equal to or a little greater than that of internarial space; anterior valve not extending inwards. Mouth a little curved. First dorsal about twice as high as long; origin a distance behind base of pelvics $1\frac{3}{4}$ to a little more than twice that between the two dorsals; base $1\frac{3}{4}$ to $2\frac{1}{4}$ in distance between dorsals. Denticles enlarged on the back, scapular region, and top of head; a series of strong compressed spines in the median line of the back, two or more on each shoulder, several round the orbits and above the spiracles, and generally a series on each rostral ridge; all the spines becoming obtuse and less prominent with age.

*Hab.* Coasts of India and Ceylon; China.

| | | |
|---|---|---|
| 1. (♀, 2150 mm.), stuffed. | Madras. | Miller. |
| 2. (♂, 400 mm.). | India. | Day. |
| 3–4. (♂, ♀, 810 & 505 mm.), stuffed. | India. | Argent Coll. |
| 5–8. (♂, ♀, 450–700 mm.), stuffed. | | |
| 9. Jaws. | India. | Boileau. |
| 10. (♂, 320 mm.), stuffed. Type of *R. spinosus*. | [Mexico?]*. | Geale. |
| 11. (♂, 1300 mm.). | Shanghai. | Swinhoe. |

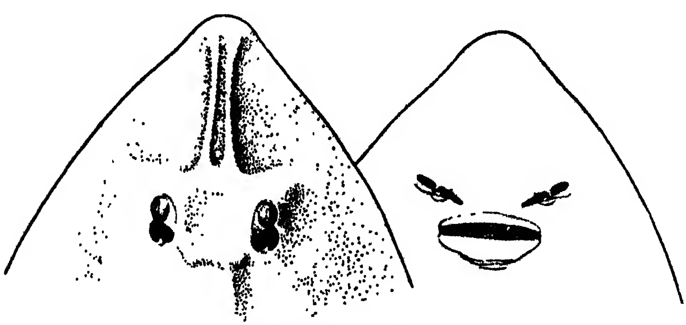
2. Rhinobatus obtusus.

*Rhinobatus* (*Rhinobatus*) *obtusus* Müller & Henle, Plagiost. p. 122, pl. 37. fig 2 (1841); Duméril, Elasmobr. p. 493 (1865).

*Rhinobatus obtusus* Günther, Cat. Fish. viii. p. 443 (1870).

*Rhinobatus halavi* Day, Fish. India, p. 731, pl. cxcii. fig. 4 (1878).

Text-figure 4.



*Rhinobatus obtusus.* (× $\frac{1}{3}$.)

Snout short, broad, obtusely pointed, the margins scarcely concave; its præorbital length about $2\frac{1}{3}$ times the distance

* The type-locality of *R. spinosus*, a species which is clearly synonymous with *R. granulatus*, is almost certainly incorrect.

between the spiracles, and its præoral length $1\frac{5}{6}$ times width of mouth. Rostral ridges rather narrow, more or less separated throughout their length, diverging a little anteriorly and posteriorly. Diameter of eye about 8 in præorbital length of snout, that of eye + spiracle $1\frac{2}{3}$ to $1\frac{3}{5}$ in distance between spiracles. Only the outer fold of the spiracle developed, weak. Nostrils rather long, oblique, twice in width of mouth, nearly equal to that of internarial space; anterior valve scarcely extending inwards. Mouth nearly straight. First dorsal nearly twice as high as long; origin a distance behind base of pelvics twice that between the two dorsals; base $2\frac{1}{4}$ to $2\frac{1}{2}$ in distance between dorsals. Denticles enlarged on the back, scapular region, and top of head; some of those in the median line of the back spinous; no distinct series of spines.

*Hab.* Coasts of India to the Malay Archipelago.

| | | |
|---|---|---|
| 1. (♀, 930 mm.). | India. | Day. |
| 2. (♀, 860 mm.), stuffed. | East Indies. | Argent Coll. |

3. Rhinobatus thouiniana.

*La raie thouin* Lacepède, Hist. Nat. Poissons, i. p. 134, pl. i. figs. 3–5 (1798).

*Raia thouiniana* Shaw, Gen. Zool. v. 2, p. 318, pl. cxlvii. fig. 2 (1804).

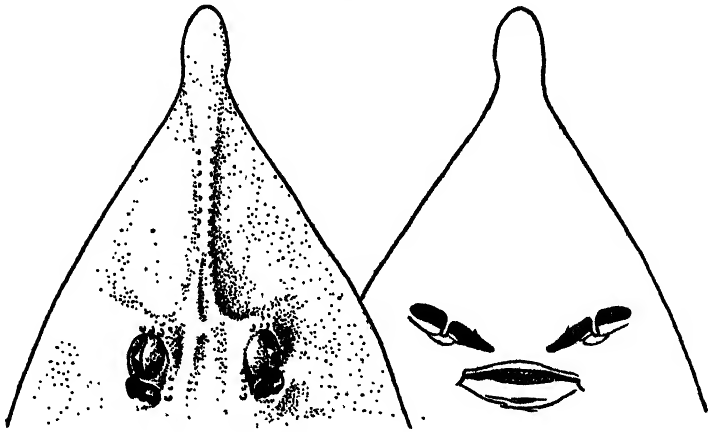
*Rhinobatus (Rhinobatus) thouini* Müller & Henle, Plagiost. p. 116 (1841); Duméril, Elasmobr. p. 500, pl. 10. fig. 2 (1865).

*Rhinobatus (Rhinobatus) ligonifer* Cantor, J. Asiat. Soc. Bengal, xviii. 1850, p. 1397, pl. xiv.; Bleeker, Verh. Bat. Gen. xxiv. 1852, Plag. p. 59.

*Rhinobatus thouini* Gray, Chondropt. p. 94 (1851); Günther, Cat. Fish. viii. p. 442 (1870); Macleay, Proc. Linn. Soc. N. S. Wales, viii. 1884, p. 280; Garman, Mem. Mus. Comp. Zool. xxxvi. 1913, p. 276.

Snout rather long, expanded at the tip, the margins distinctly concave; its præorbital length $3\frac{1}{3}$ to $3\frac{2}{5}$ times the distance between the spiracles, and its præoral length a little more than 3 times width of mouth. Rostral cartilage narrow, expanded anteriorly, the ridges approximated for the greater part of their length. Diameter of eye 8 to $8\frac{3}{4}$ in præorbital length of snout, that of eye and spiracle $1\frac{1}{3}$ to nearly $1\frac{1}{2}$ in distance between spiracles. Both folds of spiracle feebly developed, the outer the more prominent. Nostrils long, oblique, about $1\frac{1}{4}$ in width of mouth, nearly twice that of the internarial space. Anterior valve not extending inwards. Mouth nearly straight. First dorsal about twice as high as long; origin a distance behind base of pelvics $1\frac{1}{5}$ to $1\frac{1}{4}$ times that between the two dorsals; base $2\frac{1}{3}$ to $2\frac{1}{2}$ in distance between dorsals. Denticles somewhat enlarged

Text-figure 5.



*Rhinobatus thouiniana.* (× ½.)

on back, scapular region, and top of head; a series of stron compressed spines in the median line of the back, two on each shoulder, and several round the orbits and above the spiracles.

*Hab.* Red Sea (?); Malay Archipelago to New Guinea.

| | | | |
|---|---|---|---|
| 1. (♀, 405 mm.). | *R. ligonifer.* | Penang. | Cantor Coll. |
| 2. (♀, 330 mm.), skin. | *R. ligonifer.* | Penang. | Cantor Coll. |
| 3. ♂, 390 mm. | | Malay Archipelago. | Bleeker. |

4. Rhinobatus armatus.

*Rhinobatus typus* ? Bennett, in 'Life of Raffles,' p. 694 (1830).

*Rhinobatus armatus* Gray, Illust. Indian Zool. ii. pts. 13–14, pl. 99 (1834); Peters, Monatsber. Ak. Berlin, 1876, p. 853; Günther, Fische Südsee, ix. p. 492 (1910); Ogilby, Mem. Queensland Mus. iii. 1915, p. 132; *ibid.* v. 1916, p. 85, fig. 1.

*Rhinobatus* (*Rhinobatus*) *armatus* Müller & Henle, Plagiost. p. 119 (1841); Bleeker, Verh. Bat. Gen. xxiv. 1852, Plag. p. 60; Nat. Tijdschr. Ned. Ind. iii. 1852, p. 85; Duméril, Elasmobr. p. 494, pl. 10. fig. 4 (1865).

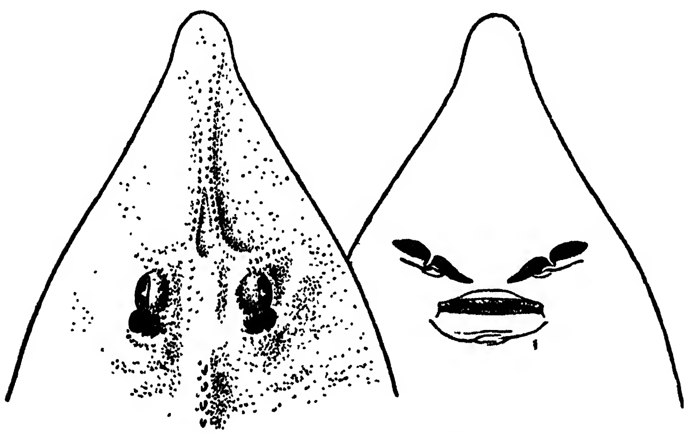
*Rhinobatus granulatus* (part.) Günther, Cat. Fish. viii. p. 443 (1870); Day, Fish. India, p. 732 (1878).

*Rhinobatus halavi* Garman, Mem. Mus. Comp. Zool. xxxvi. 1913, p. 275.

Snout moderate, bluntly pointed, the margins scarcely concave; its præorbital length 3 to 3½ times the distance between the spiracles, and its præoral length about 3 times width of mouth. Rostral ridges narrow, closely approximated for the greater part of their length, diverging a little posteriorly. Diameter of eye

$6\frac{1}{4}$ to $8\frac{1}{2}$ in præorbital length of snout, that of eye + spiracle $1\frac{1}{4}$ to $1\frac{2}{5}$ in distance between spiracles. Both folds of spiracles feebly developed, the outer the more prominent. Nostrils long, oblique, $\frac{5}{6}$ of or nearly equal to width of mouth, $2\frac{1}{4}$ to $2\frac{2}{5}$ times that of internarial space; anterior valve not extending inwards. Mouth nearly straight. First dorsal twice or more than twice as high as long; origin a distance behind base of pelvics $1\frac{1}{3}$ to $1\frac{3}{5}$ times that between the two dorsals; base 2 to $2\frac{1}{4}$ in distance

Text figure 6.



*Rhinobatus armatus.* (× ½.)

between dorsals. Denticles somewhat enlarged on the back, scapular region, and top of head; a series of fairly strong compressed spines in the median line of the back, one or two groups on each shoulder, and several smaller spines round the orbits and above the spiracles.

*Hab.* Indian Ocean; Malay Peninsula and Archipelago to Australia and the Solomon Islands.

| | | |
|---|---|---|
| 1. (♀, 420 mm.). | India. | Hardwicke. |
| 2. (♂, 520 mm.). | Singapore. | Morton. |
| 3–4. (♂, ♀, 470 & 550 mm.). | Macassar. | Meyer. |
| 5. (♂, 360 mm.), stuffed. *R. typus*? | Sumatra. | Raffles Coll. |
| 6. (♀, 390 mm.). | C. York, N. Australia. | Dämel. |
| 7. (♂, 350 mm.). | Groote Eylandt, N.W. Territory, Australia. | Wilkins. |
| 8. (♂, 480 mm.). | Western Australia. | Montague. |

5. Rhinobatus cemiculus.

*Raja rhinobatos* (*non* Linn.) Shaw, Gen. Zool. v. 2, p. 317, pl. cxlvii. fig. 1 (1804).

*Rhinobatus cemiculus* Geoffroy St. H., in Savigny, Egypte, i. (1) [Poissons Mer Rouge et Medit.], p. 338, pl. 27. fig. 3 (1827); Müller & Henle, Plagiost. p. 118 (1841); Duméril, Elasmobr. p. 495, pl. 10. fig. 3 (1865); Carus, Prod. Faun. Medit. ii. p. 516 (1889–93).

*Glaucostegus cemiculus* Bonaparte, Cat. Metod. Pesci Europ. p. 14 (1846).

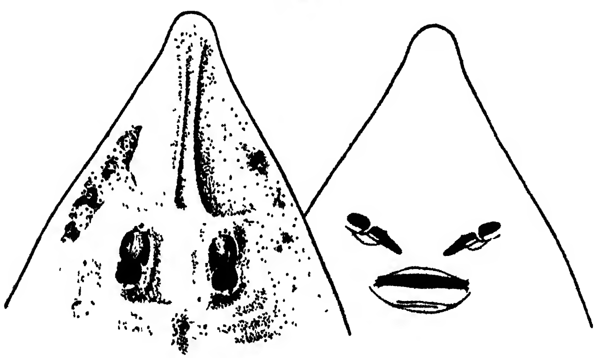
*Rhinobatus halavi* Guichenot, Explor. Algér., Poissons, p. 129 (1850); Doderlein, Natur. Sicil. iii. 1884, p. 169; Carus, Prod. Faun. Medit. ii. p. 515 (1889–93); Carruccio, Boll. Soc. Zool. Ital. ser. 2, ix. 1901, p. 97; Lozano y Rey, Mem. Soc. Esp. Hist. Nat. xii. 1921, p. 147, pl. ii. figs. 3–4.

*Rhinobatus halavi* (part.) Günther, Cat. Fish. viii. p. 442 (1870).

*Rhinobatus halavi*? Vinciguerra, Ann. Mus. Civ. St. Nat. Genova, xx. 1884, p. 412.

Snout moderate, bluntly pointed, the margins straight or very little concave; its præorbital length about 3 times the distance

Text-figure 7.



*Rhinobatus cemiculus.* (× $\frac{1}{3}$.)

between the spiracles, and its præoral length $2\frac{2}{3}$ to $2\frac{4}{5}$ times width of mouth. Distance from tip of snout to anterior edge of eye rather less than that from hinder edge of eye to axil of pectoral in adults. Rostral ridges narrow, close together and nearly parallel anteriorly, diverging posteriorly. Diameter of eye $5\frac{5}{6}$ to $6\frac{1}{3}$ in præorbital length of snout, that of eye + spiracle $1\frac{1}{4}$ to $1\frac{1}{3}$ in distance between spiracles. Both folds of spiracle developed, the inner very small. Nostrils of moderate length, oblique, $1\frac{2}{5}$ to $1\frac{1}{2}$ in width of mouth, $1\frac{1}{3}$ to $1\frac{1}{2}$ times that of internarial space; anterior valve not or scarcely extending inwards. Mouth nearly straight. First dorsal about twice as high as long; origin a distance behind base of pelvics equal to or

nearly equal to that between the two dorsals; base $2\frac{1}{2}$ to $2\frac{3}{4}$ in distance between dorsals. Skin covered with small denticles; a series of strong compressed spines in the median line of the back, a pair on each shoulder arranged thus :, and several smaller spines round the orbits and above the spiracles; young individuals with a series of small spines on each rostral ridge. Sometimes a black blotch below the end of the snout.

*Hab.* Mediterranean.

| | | | |
|---|---|---|---|
| 1. | (♀, 775 mm.), stuffed. | | Zool. Soc. Coll. |
| 2. | (♂, 585 mm.). | | Haslar Coll. |
| 3. | (♂, 500 mm.). | Gemileh, Egypt. | C. U. Suez Canal Exped. |
| 4. | (♂, 280 mm.). | L. Menzaleh, Egypt. | Mitchell. |

In addition to the specimens listed above, two immature males (315 and 385 mm.) from Port Said and Tunis, lent to me by Dr. Vinciguerra, have been included in the description of the species.

I am much indebted to Mr. P. Chabanaud, of the Paris Museum, for a photograph of the type of *R. cemiculus*.

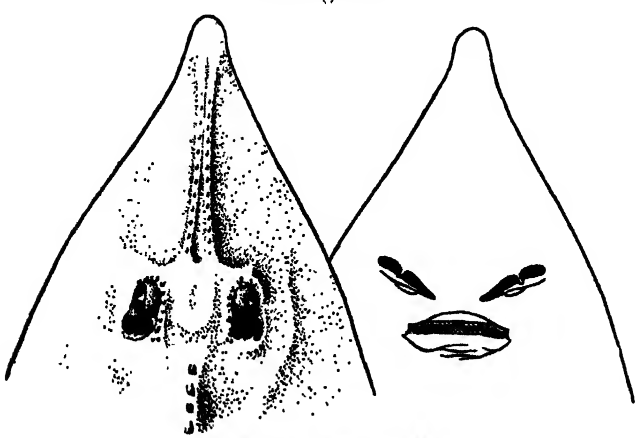
6. Rhinobatus rasus.

*Rhinobatus halavi* (part.) Günther, Cat. Fish. viii. p. 442 (1870).

*Rhinobatus rasus* Garman, Bull. Mus. Comp. Zool. li. 1908, p. 253; Mem. Mus. Comp. Zool. xxxvi. 1913, p. 270, pl. 17 *a*. figs. 1–2.

Perhaps not distinct from *R. cemiculus*. Snout a little longer,

Text-figure 8.



*Rhinobatus rasus.* (× $\frac{1}{2}$.)

its præorbital length nearly $3\frac{1}{3}$ times the distance between the spiracles, and its præoral length 3 times width of mouth.

Distance from tip of snout to anterior edge of eye about equal to that from hinder edge of eye to axil of pectoral. Diameter of eye about 8 in præorbital length of snout, that of eye + spiracle $1\frac{1}{3}$ in distance between spiracles. Two spines on each shoulder, a single one corresponding to the pair present in *R. cemiculus*, and another smaller one placed more laterally. A faint dark blotch below the end of the snout.

*Hab.* West Africa.

| | | |
|---|---|---|
| 1. (♀, 750 mm.), skin. | Gambia. | |
| 2. (♀, 430 mm.). | R. Bonny. | Wood. |

7. RHINOBATUS HALAVI.

*Raja halavi* Forskal, Descr. Anim. p. 19 (1775).

*Rhinobatus halavi* Rüppell, Fische Roth. Meers, p. 55, pl. 14. fig. 2 (1828); Klunzinger, Synopsis Fische Roth. Meeres, ii. p. 235 (1871); Kossman & Rauber, Pisces, in Kossman, Zool. Ergeb. Reise Roth. Meeres, p. 32 (1877).

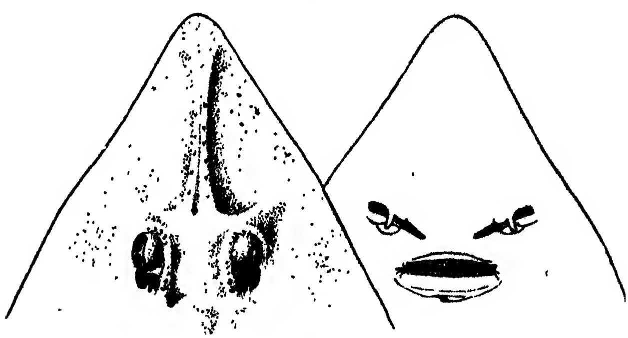
*Rhinobatus (Rhinobatus) halavi* Müller & Henle, Plagiost. p. 120 (1841); Duméril, Elasmobr. p. 496 (1865).

*Rhinobatus halavi* (part.) Günther, Cat. Fish. viii. p. 442 (1870).

*Rhinobatus granulatus* Bamber, J. Linn. Soc., Zool. xxxi. 1915, p. 477.

Snout moderate, bluntly pointed, the margins nearly straight; its præorbital length $2\frac{3}{4}$ to 3 times the distance between the

Text-figure 9.



*Rhinobatus halavi.* (× $\frac{1}{3}$.)

spiracles, and its præoral length $2\frac{3}{5}$ to $2\frac{2}{3}$ times width of mouth. Rostral ridges rather narrow, more or less approximated for the greater part of their length, diverging a little anteriorly and posteriorly. Diameter of eye 5 to 6 in præorbital length of snout, that of eye + spiracle $1\frac{1}{3}$ to $1\frac{1}{2}$ in distance between spiracles. Outer fold of spiracle moderate, inner small. Nostrils

of moderate length, oblique, about $1\frac{1}{2}$ in width of mouth, $1\frac{1}{3}$ to $1\frac{1}{2}$ times that of internarial space; anterior valve scarcely extending inwards. Mouth nearly straight. First dorsal twice as high as long; origin a distance behind base of pelvics $1\frac{2}{3}$ to nearly twice that between the two dorsals; base $2\frac{2}{5}$ to $2\frac{1}{5}$ in distance between dorsals. Denticles enlarged on the back, scapular region, and top of head; a series of compressed spines in the median line of the back, becoming more obtuse and irregular with age, one or two on each shoulder, and several smaller ones round the orbits and above the spiracles; young individuals with a series of small spines on each rostral ridge.

*Hab.* Red Sea and Persian Gulf; China.

| | | |
|---|---|---|
| 1-2. (♂, ♀, 300 & 500 mm.). | Red Sea. | Bisbee. |
| 3. (♂, 700 mm.), stuffed. | Red Sea. | Ruppell. |
| 4. (♀, 1500 mm.), stuffed. | Muscat. | Jayaker. |
| 5. (♀, 890 mm.), stuffed. | China. | |

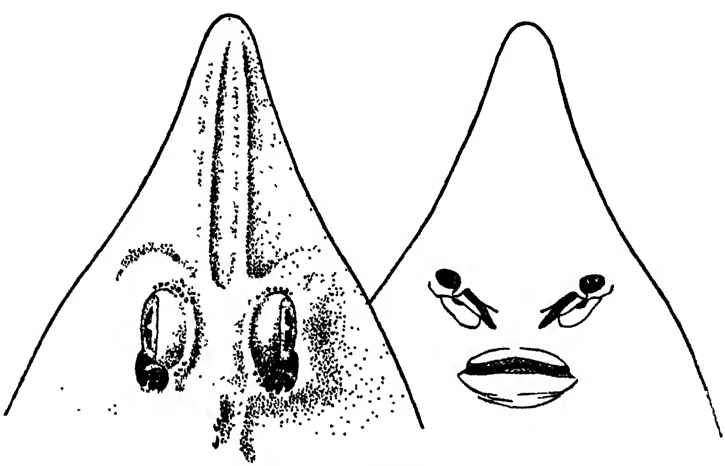
8. RHINOBATUS HOLCORHYNCHUS.

*Rhinobatus holcorhynchus* Norman, Ann. Mag. Nat. Hist. ser. 9, ix. 1922, p. 318; Barnard, Ann. S. African Mus. xxi. 1925, p. 61, pl. iii. fig. 7, text-fig.

*Rhinobatus natalensis* Fowler, Ann. Natal Mus. v. 1925, p. 195, fig. 1.

*Rhinobatus rasus* Fowler, Proc. Acad. Nat. Sci. Philad. lxxvii. 1925, p. 192.

Text-figure 10.



*Rhinobatus holcorhynchus.* (× $\frac{1}{3}$.)

Snout long, bluntly pointed, the margins somewhat concave; its præorbital length $2\frac{2}{3}$ times the distance between the spiracles,

and its præoral length $3\frac{1}{3}$ times width of mouth. Rostral ridges narrow, widely separated and nearly parallel throughout their length, converging a little anteriorly. Diameter of eye $4\frac{1}{5}$ in præorbital length of snout, that of eye + spiracle equal to the distance between spiracles. Outer fold of spiracle moderate, inner small. Nostrils long, oblique, $1\frac{1}{4}$ in width of mouth, $1\frac{4}{5}$ times that of internarial space; anterior valve extending inwards as far as level of inner edge of nostril. Mouth nearly straight. First dorsal twice as high as long; origin a distance behind base of pelvics $1\frac{1}{3}$ times in that between the two dorsals; base $3\frac{2}{3}$ in distance between dorsals. Skin smooth; a series of blunt tubercles in the median line of the back, a group of three or four on each shoulder, and some smaller ones round the orbits and above the spiracles. A dark blotch below the end of the snout.

*Hab.* Natal and Zululand.

1. (♂, 700 mm.). Type of the species. Zululand Coast, 45 fms. Marley.

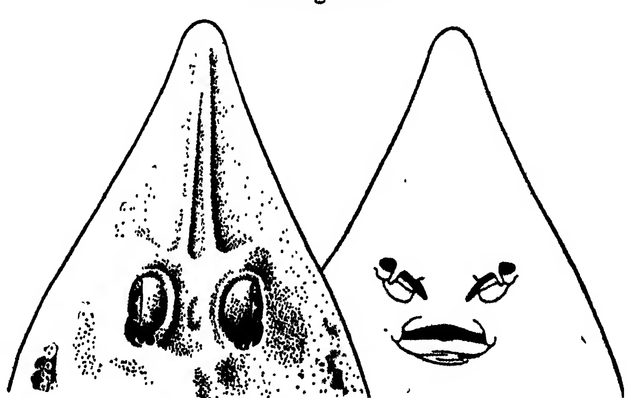
9. RHINOBATUS FORMOSENSIS, sp. n.

*Rhinobatus schlegelii* (part.) Günther, Cat. Fish. viii. p. 445 (1870).

? *Rhinobatus schlegelii* Garman, Mem. Mus. Comp. Zool. xxxvi. 1913, p. 276.

Snout long, bluntly pointed, the margins straight or a little concave; its præorbital length a little more than 3 times the

Text-figure 11.



*Rhinobatus formosensis.* (× $\frac{1}{3}$)

distance between the spiracles, and its præoral length $3\frac{3}{5}$ to $3\frac{2}{3}$ times width of mouth. Rostral ridges rather narrow, more or less separated throughout their length, nearly parallel anteriorly,

diverging a little posteriorly. Diameter of eye $4\frac{1}{3}$ to $4\frac{2}{3}$ in præorbital length of snout, that of eye + spiracle nearly equal to distance between spiracles. Outer fold of spiracle well developed, inner small. Nostrils of moderate length, oblique, $1\frac{4}{5}$ to $1\frac{1}{3}$ in width of mouth, about $1\frac{1}{2}$ times that of internarial space; distance from lateral margin of snout (measured horizontally) a little less than length of nostril; anterior valve extending inwards nearly as far as level of inner edge of nostril. Mouth nearly straight. First dorsal nearly twice as high as long; origin a distance behind base of pelvics equal to or greater than that between the two dorsals; base 3 to $3\frac{1}{4}$ in distance between dorsals. Skin covered with minute denticles, smooth to the touch; a series of rudimentary tubercles in the median line of the back, round the orbits and above the spiracles, scarcely discernible without the aid of a lens.

*Hab.* Formosa.

1-2. (♂, 625 & 630 mm.). Types of the species. Formosa. Swinhoe.

10. RHINOBATUS SCHLEGELII.

*Rhinobatus* (*Rhinobatus*) *schlegelii* Müller & Henle, Plagiost. p. 123, pl. 42 (1841); Duméril, Elasmobr. p. 497 (1865).

*Rhinobatus schlegelii* Richardson, Rep. Brit. Ass. for 1845 (1846), p. 195; Schlegel, Faun. Japon. p. 307 (1850); Bleeker, Act. Soc. Sci. Indo-Neerl. iii. 1858, Japan, p. 41; Pietschmann, Sitzber. K. Ak. Wiss. cxvii. Abt. 1, 1908, p. 15.

*Rhinobatus schlegelii* (part.) Günther, Cat. Fish. viii. p. 445 (1870).

*Rhinobatus schlegel* (part.) Jordon & Fowler, Proc. U.S. Nat. Mus. xxvi. 1903, p. 645.

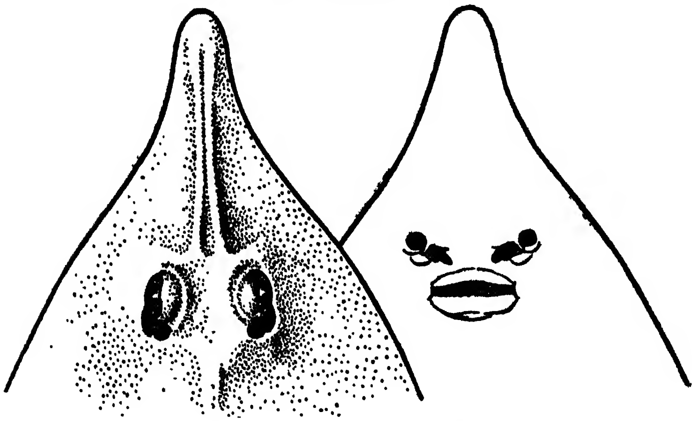
Snout long, bluntly pointed, the margins concave; its præorbital length $3\frac{1}{4}$ times the distance between the spiracles, and its præoral length $3\frac{1}{3}$ times width of mouth. Rostral ridges rather narrow, parallel and approximated anteriorly, diverging a little posteriorly. Diameter of eye nearly 5 in præorbital length of snout, that of eye + spiracle nearly equal to distance between spiracles. Both folds of spiracle feebly developed, the outer the more prominent. Nostrils rather short, oblique, $1\frac{2}{3}$ in width of mouth, $1\frac{1}{3}$ times that of internarial space; distance from lateral margin of snout greater than length of nostril; anterior valve extending inwards nearly as far as level of inner edge of nostril. Mouth nearly straight. First dorsal about twice as high as long; origin a distance behind base of pelvics a little greater than that between the two dorsals; base about 3 in distance between dorsals. Skin covered with minute denticles, smooth to the touch; a series of small blunt tubercles in the median line of the back, round the orbits, and above the spiracles. A black blotch below the end of the snout.

*Hab.* China and Japan.

1. (♀, 370 mm.). Japan. Jamrach.

The species of *Rhinobatus* from Japan appear to have been somewhat confused. Some of the records of *R. schlegelii* probably refer to *R. polyophthalmus* or *R. formosensis*.

Text-figure 12.



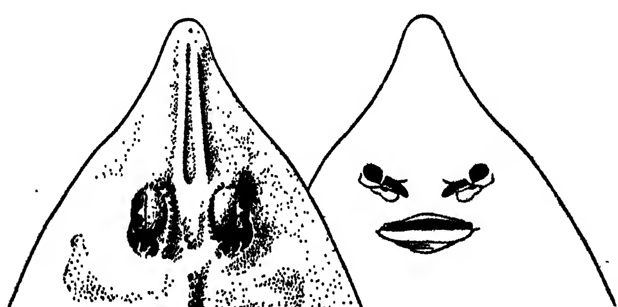
*Rhinobatus schlegelii.* (× ½.)

I am greatly indebted to Dr. C. Popta for photographs of the types of *R. schlegelii* and *R. polyophthalmus* (Bleeker Collection) in the Leiden Museum.

11. RHINOBATUS ANNANDALEI, sp. n.

*Rhinobatus columnæ* (*non* Bonaparte) Annandale, Mem. Ind. Mus. ii. 1909, p. 14.

Text-figure 13.



*Rhinobatus annandalei.* (× ⅓.)

Snout moderate, bluntly pointed, the margins a little concave; its præorbital length about 2½ times the distance between the

spiracles, and its præoral length $2\frac{1}{3}$ to $2\frac{1}{2}$ times width of mouth. Rostral ridges more or less separated throughout their length, parallel anteriorly, diverging a little posteriorly. Diameter of eye $3\frac{2}{5}$ to $3\frac{4}{5}$ in præorbital length of snout, that of eye + spiracle a little greater than distance between spiracles. Both folds of spiracle strongly developed, the outer the more prominent. Nostrils of moderate length, $1\frac{4}{5}$ in width of mouth, about $1\frac{2}{5}$ times that of internarial space; anterior valve extending inwards to level of inner edge of nostril or a little beyond. Mouth nearly straight. First dorsal a little more than twice as high as long; origin a distance behind base of pelvics $1\frac{1}{4}$ to $1\frac{1}{3}$ in that between the two dorsals; base $2\frac{1}{4}$ to $2\frac{2}{5}$ in distance between dorsals. Skin covered with minute denticles, rather smooth to the touch; a series of fairly small and close-set spines in the median line of the back, two to four on each shoulder, and several round the orbits and above the spiracles; all the spines stronger and sharper in the male.

*Hab.* Bengal.

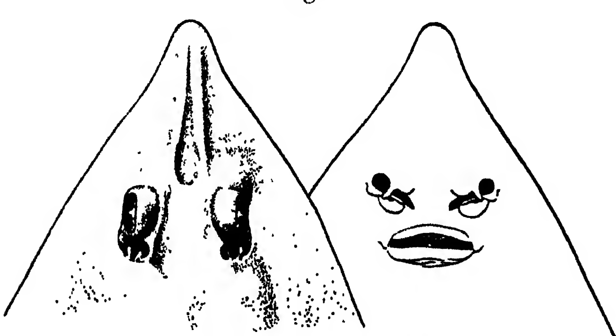
| | | |
|---|---|---|
| 1, 2. (♂, ♀, 415 & 395 mm.). Types of the species. | East Channel, mouth of R. Hughli, 40 fms. | Indian Museum. |

12. Rhinobatus lionotus, sp. n.

*Rhinobatus schlegelii* (*non* Müller & Henle), Annandale, Mem. Ind. Mus. ii. 1909, p. 15.

Snout moderate, bluntly pointed, the margins scarcely concave; its præorbital length $2\frac{1}{3}$ times the distance between the spiracles,

Text-figure 14.



*Rhinobatus lionotus.* (× $\frac{1}{3}$.)

and its præoral length $2\frac{2}{5}$ times width of mouth. Rostral ridges more or less separated throughout their length, parallel anteriorly, diverging posteriorly. Diameter of eye $3\frac{2}{5}$ in præorbital length of snout, that of eye and spiracle about equal to distance between spiracles. Both folds of spiracles very strongly developed, the

outer the more prominent. Nostrils of moderate length, oblique, $1\frac{2}{3}$ in width of mouth, $1\frac{1}{3}$ times that of internarial space; anterior valve extending inwards about to level of inner edge of nostril. Mouth nearly straight. First dorsal twice as high as long; origin a distance behind base of pelvics about equal to that between the two dorsals; base $2\frac{4}{5}$ in distance between dorsals. Skin covered with minute denticles, smooth to the touch; a series of minute tubercles in the median line of the back, a single one on each shoulder, and several round the orbits and above the spiracles.

*Hab.* Bengal.

| | | |
|---|---|---|
| 1. (♀, 500 mm.). Type of the species. | East Channel, mouth of R. Hughli, 40 fms. | Indian Museum. |

13. RHINOBATUS HYNNICEPHALUS.

*Rhinobatus hynnicephalus* Richardson, Rep. Brit. Ass. for 1845 (1846), p. 195; Garman, Mem. Mus. Comp. Zool. xxxvi. 1913, p. 274.

*Rhinobatus (Syrrhina) polyophthalmus* Bleeker, Nat. Tijdschr. Ned. Ind. vi. 1854, p. 423; Verh. Bat. Gen. xxvi. 1854-7, Japan, p. 129.

*Raja (Syrrhina) columnæ* Bleeker, Ned. Tijdschr. Dierk. ii. 1865, p. 271; *ibid.* iv. 1873, p. 120.

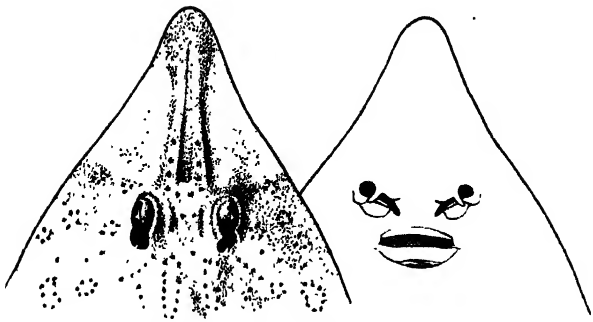
*Rhinobatus polyophthalmus* Bleeker, Act. Soc. Sci. Indo-Neerl. iii. 1857, Japan, pl. iv.; Jordon & Fowler, Proc. U.S. Nat. Mus. xxvi. 1903, p. 646; Garman, Mem. Mus. Comp. Zool. xxxvi. 1913, p. 274.

*Rhinobatus schlegelii* (part.) Günther, Cat. Fish. viii. p. 445 (1870).

*Rhinobatus columnæ* Steindachner, Ann. Nat. Hofmus. Wien, xi. 1896, p. 225.

Snout moderate, bluntly pointed, the margins scarcely concave; its præorbital length $2\frac{2}{5}$ to $2\frac{1}{2}$ times the distance between the spiracles, and its præoral length about 3 times width of mouth. Rostral ridges rather broad, narrowly separated anteriorly, diverging a little posteriorly. Diameter of eye $4\frac{2}{3}$ to $5\frac{4}{5}$ in præorbital length of snout, that of eye + spiracle $1\frac{1}{5}$ to $1\frac{1}{4}$ in distance between spiracles. Outer fold of spiracle moderately developed, inner rudimentary or absent. Nostrils of moderate length, oblique, $1\frac{1}{2}$ to $1\frac{3}{5}$ in width of mouth, about $1\frac{1}{4}$ times that of internarial space; anterior valve extending inwards to level of inner edge of nostril or a little beyond. Mouth nearly straight. First dorsal about twice as high as long; origin a distance behind base of pelvics $1\frac{1}{5}$ to $1\frac{1}{4}$ times that between the two dorsals; base $2\frac{1}{2}$ to nearly 3 in distance between dorsals. Skin covered with minute denticles, smooth to the touch; a series of very small, blunt tubercles in the median line of the back, and a few round the orbits and above the spiracles. Back brownish, with groups of small blackish-brown spots, sometimes forming oval or rounded

Text-figure 15.



*Rhinobatus hynnicephalus.* (× ⅓.)

rings; the markings tend to become less conspicuous in older examples; young with a faint dark blotch below the end of the snout.

*Hab.* China and Japan.

| | | |
|---|---|---|
| 1. (♀, 700 mm.). | Japan. | Jamrach. |
| 2. (♂, 610 mm.). | Hiroshima, Japan. | Jordan. |
| 3. (♀, 520 mm.). | Inland Sea of Japan. | Gordon Smith |
| 4. (♂, 330 mm.). | Inland Sea of Japan. | Gordon Smith. |

Richardson's species (*R. hynnicephalus*) was based on an illustration in the collection of water-colour drawings of Chinese fishes made by Mr. J. Reeves [plate 119, No. A 7]. I have compared this figure with a photograph of the type of *R. polyophthalmus* in the Leiden Museum, and conclude that the two species are synonymous.

14. Rhinobatus rhinobatus.

*Raja rhinobatus* Linnæus, Syst. Nat., Ed. 10, p. 232 (1758).

*Raja rostrata* Shaw, Nat. Misc. v. pl. 173 (1794).

*Rhinobatus rhinobatus* (part.) Bloch, Schneider, Syst. Ichth. p. 353 (1801); Garman, Mem. Mus. Comp. Zool. xxxvi. 1913, p. 270.

*Leiobatus panduratus* Rafinesque, Caratteri, p. 16 (1810); Indice, p. 48, no. 361 (1810).

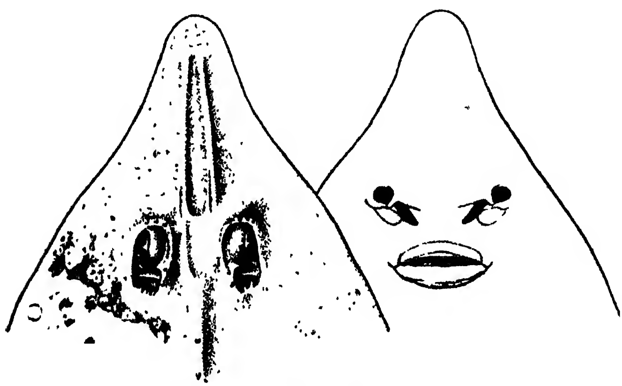
*Rhinobatus vulgaris* Cloquet, Dict. Sci. Nat. xlv. 1827, p. 326.

*Rhinobatus columnæ* Bonaparte, Icon. Fauna Ital. iii. Pesca, [14, 17] (1835–6); Costa, Fauna Reg. Napoli, Pesci, 3, pl. x. (1850); Steindachner, Denkschr. Ak. Wiss. xlv. 1882, p. 14; Vinciguerra, Ann. Mus. Civ. St. Nat. Genova, xx. 1884, p. 312; Pietschmann, Ann. Nat. Hofmus. Wien, xxi. 1906, p. 129; Lozano y Rey, Mem. Soc. Esp. Hist. Nat. xii. 1921, p. 146, pl. ii. figs. 1–2.

*Rhinobatus (Syrrhina) columnæ*, Müller & Henle, Plagiost. p. 113 (1841); Duméril, Elasmobr. p. 486 (1865).

Snout moderate, bluntly pointed, the margins a little concave; its præorbital length nearly 3 times the distance between the spiracles, and its præoral length $2\frac{4}{5}$ times width of mouth. Rostral ridges narrow, separated throughout their length, converging a little anteriorly, parallel posteriorly. Diameter of eye a little more than 5 in præorbital length of snout, that of eye + spiracle a little less than distance between spiracles. Both folds of spiracle moderately developed, the outer the more prominent. Nostrils of moderate length, oblique, $1\frac{3}{5}$ in width of mouth, $1\frac{1}{4}$? times that of internarial space; anterior valve extending

Text-figure 16.



*Rhinobatus rhinobatus.* (× $\frac{1}{4}$.)

inwards a little beyond level of inner edge of nostril. Mouth nearly straight. First dorsal about twice as high as long; origin a distance behind base of pelvics a little less than that between the two dorsals; base $2\frac{3}{4}$ in distance between dorsals. Skin covered with minute denticles, rather smooth to the touch; a series of small, compressed spines in the median line of the back, three on each shoulder, and several smaller ones round the orbits and above the spiracles.

*Hab.* Mediterranean; West Africa (*Steindachner*).

The above description is based on a single specimen (♂, 545 mm.) from Tunis, lent to me by Dr. L. Vinciguerra.

15. Rhinobatus annulatus.

*Rhinobatus* (*Syrrhina*) *annulatus* Müller & Henle, Plagiost. p. 116 (1841); Smith, Illust. Zool. S. Africa, Pisces, pl. xvi. (1842); Duméril, Elasmobr. p. 487, pl. 10. fig. 6 (1865).

*Rhinobatus annulatus* Kner, Reise 'Novara,' Zool. i. 5 Fische, p. 416 (1869); Garman, Mem. Mus. Comp. Zool. xxxvi. 1913, p. 271; Bonde & Swart, Fish. Mar. Survey S.A. iii. Spec. Rep.

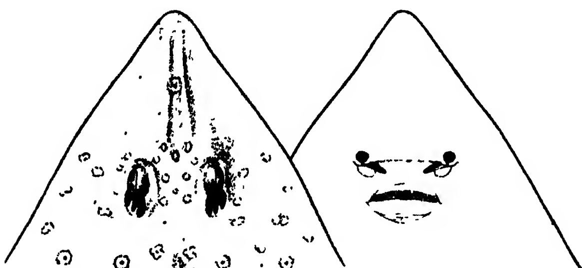
v. 1923, p. 3; Barnard, Ann. S. African Mus. xxi. 1925, p. 59, text-fig. 9 *a*.

*Rhinobatus columnæ* (part.) Günther, Cat. Fish. viii. p. 446 (1870).

*Rhinobatus blochii* (part.) Regan, Ann. Natal Gov. Mus. i. 1908, p. 242.

Snout moderate, bluntly pointed, the margins straight or very little concave; its præorbital length $2\frac{1}{3}$ to $2\frac{3}{5}$ times the distance between the spiracles, and its præoral length $2\frac{3}{4}$ to 3 times width of mouth. Rostral ridges rather narrow, separated throughout their length, parallel or converging a little anteriorly, diverging

Text-figure 17.



*Rhinobatus annulatus* (× $\frac{1}{6}$)

posteriorly. Diameter of eye 5 to $5\frac{1}{4}$ in præorbital length of snout, that of eye + spiracle $1\frac{1}{5}$ to $1\frac{1}{4}$ in distance between spiracles. Both folds of spiracle well developed, the outer the more prominent. Nostrils of moderate length, oblique, $1\frac{3}{4}$ to nearly twice in width of mouth, about equal to that of internarial space; distance from lateral margin of snout 3 to $3\frac{3}{5}$ in præoral length of snout; anterior valve extending inwards well beyond level of inner edge of nostril, nearly meeting that of opposite side. Mouth nearly straight. First dorsal nearly twice as high as long; origin a distance behind base of pelvics about equal to that between the two dorsals; base $2\frac{1}{3}$ to nearly 3 in distance between dorsals. Skin covered with minute denticles, rather smooth to the touch; a series of small, compressed spines in the median line of the back, in one or two groups on each shoulder, and some smaller spines round the orbits and above the spiracles; all the spines becoming less prominent with age. Upper surface of body with dark annular ocelli, the largest of which are smaller than the eye.

*Hab.* South Africa.

| | | |
|---|---|---|
| **1. (♀, 1020 mm.), stuffed. Type of the species.** | **Cape of Good Hope.** | **Smith.** |
| **2. (♀, 930 mm.).** | **Cape of Good Hope.** | **Gerrard.** |
| **3. (♂, 440 mm.).** | **Port Natal.** | **Ayres.** |
| **4. (♀, 880 mm.).** | **Bird Isd., Algoa Bay.** | **Warren.** |
| **5. (♀, 780 mm.).** | **Zululand Coast, 40–50 fms.** | **Marley.** |

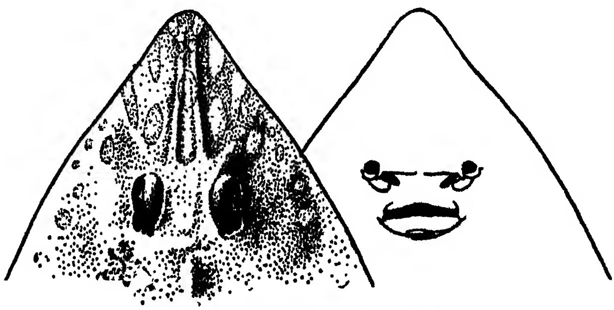
16. RHINOBATUS LEUCOSPILUS, sp. n.

*Rhinobatus blochii* (part.) Regan, Ann. Natal Gov. Mus. i. 1908, p. 242.

?*Rhinobatus blochii* Gilchrist & Thompson, Ann. S. African Mus. xi. 1911, p. 55.

Very close to the preceding species, but with the snout rather shorter and broader; its præorbital length 2 to 2¼ times the distance between the spiracles, and its præoral length 2½ to 2¾ times width of mouth. Diameter of eye 3½ to 4 in præorbital length of snout, that of eye and spiracle a little less than distance between spiracles. Distance between outer edge of nostril and lateral margin of snout 2½ to 2¾ in præoral length of snout. Spines on back and shoulders minute. Back brownish, the margins of the pectoral and pelvic fins bluish grey; snout and pectoral fins with a number of pale bluish-grey spots and blotches symmetrically arranged.

Text-figure 18.



*Rhinobatus leucospilus.* (× ⅜.)

*Hab.* Natal.

| | | | |
|---|---|---|---|
| 1. (♂, 415 mm.). | Type of the species. | Durban. | Warren. |
| 2. (♂, 250 mm.). | Type of the species. | Durban. | Marley. |

17. RHINOBATUS ZANZIBARENSIS, sp. n.

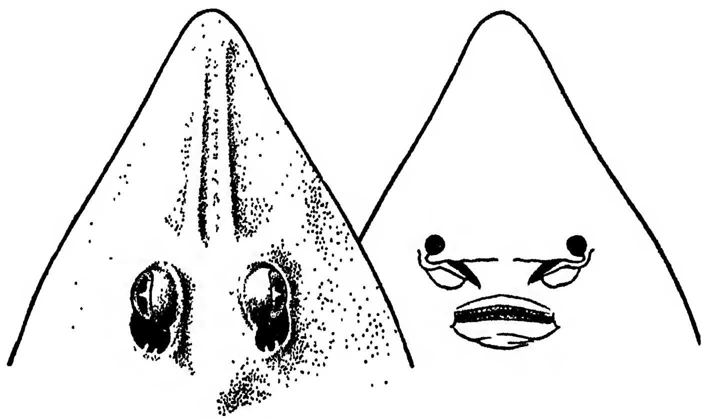
*Rhinobatus schlegelii* (*non* Müller & Henle), Playfair & Günther, Fish. Zanzibar, p. 142 (1866).

*Rhinobatus columnæ* (part.) Günther, Cat. Fish. viii. p. 446 (1870).

Snout moderate, bluntly pointed, the margins straight; its præorbital length nearly 3 times the distance between the spiracles, and its præoral length about 3 times width of mouth, which is 7½ in distance from tip of snout to anterior edge of vent. Rostral ridges rather broad, separated throughout their length, almost parallel. Diameter of eye about 4½ in præorbital length of snout, that of eye + spiracle about equal to distance between

spiracles. Both folds of spiracle well developed, the outer the more prominent. Nostrils rather long, oblique, nearly $1\frac{1}{2}$ in width of mouth, $1\frac{1}{2}$ times that of internarial space; distance between outer edge of nostril and lateral margin of snout more than 4 times in præoral length of snout; anterior valve extending inwards well beyond level of inner edge of nostril, separated from that of opposite side by a distance which is $2\frac{3}{4}$ to 3 in internarial

Text-figure 19.



*Rhinobatus zanzibarensis.* ($\times \frac{1}{3}$.)

width. Mouth nearly straight. First dorsal about $1\frac{1}{2}$ times as high as long; origin a distance behind base of pelvics $1\frac{1}{3}$ to $1\frac{1}{2}$ times that between the two dorsals; base $2\frac{5}{6}$ in distance between dorsals. Skin covered with minute denticles; a series of very small, blunt spines in the median line of the back, in two groups on each shoulder, and some smaller spines round the orbits and above the spiracles.

*Hab.* Zanzibar.

| | | | |
|---|---|---|---|
| 1. (♂, 750 mm.). | Type of the species. | Zanzibar. | Playfair. |
| 2. (♀, 2050 mm.), stuffed. | | Zanzibar. | Playfair. |

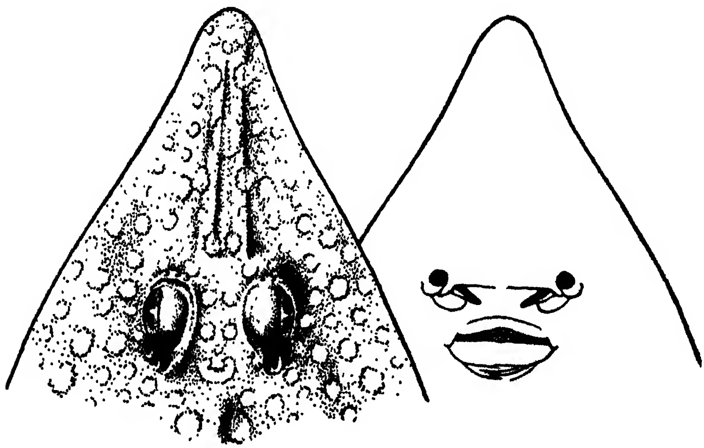
18. RHINOBATUS OCELLATUS, sp. n.

*Rhinobatus columnæ* (*non* Bonaparte), Regan, Ann. Natal Gov. Mus. i. 1908, p. 242.

Close to *R. zanzibarensis.* Præoral length of snout $3\frac{1}{2}$ times width of mouth, which is more than 8 times in distance from tip of snout to anterior edge of vent. Nostrils of moderate length, oblique, $1\frac{3}{5}$ in width of mouth, $1\frac{1}{2}$ times that of internarial space; distance between outer edge of nostril and lateral margin of snout about $3\frac{4}{5}$ in præoral length of snout; anterior valve

extending inwards well beyond level of inner edge of nostril, separated from that of opposite side by a distance which is 3½ in internarial width. First dorsal about twice as high as long; origin a distance behind base of pelvics a little greater than that between the two dorsals; base 3⅝ in distance between dorsals.

Text-figure 20.



*Rhinobatus ocellatus.* (× ⅓.)

Skin covered with minute denticles; a series of small, blunt spines in the median line of the back, a single pair on each shoulder, and a few spines round the orbits and above the spiracles. Back brownish, with numerous bluish-grey ocelli, the largest of which are smaller than the eye.

*Hab.* South Africa.

1. (♂, 700 mm.). Type of the species. Bird Isd., Algoa Bay. Warren.

19. Rhinobatus blochii.

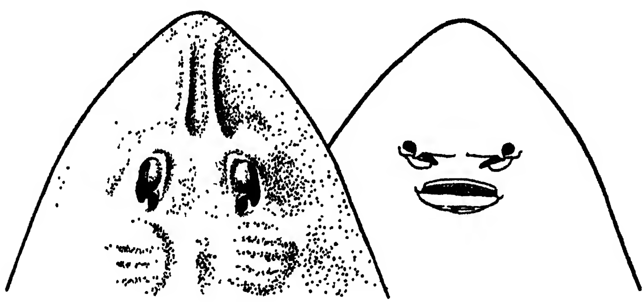
*Rhinobatus* (*Syrrhina*) *blochii* Müller & Henle, Plagiost. p. 115, pl. 37. fig. 1 (1841); Duméril, Elasmobr. p. 488, pl. 10. fig. 5 (1865).

*Rhinobatus blochii* Günther, Cat. Fish. viii. p. 447 (1870); Garman, Mem. Mus. Comp. Zool. xxxvi. 1913, p. 271; Bonde & Swart, Fish. Mar. Survey S.A. iii. Spec. Rep. v. 1923, p. 3; Barnard, Ann. S. African Mus. xxi. 1925, p. 61, text-fig. 9 *b*.

Snout short, broad, obtusely pointed, the margins somewhat convex; its præorbital length 1⅝ to 1⅞ times the distance between the spiracles, and its præoral length 2¼ to 2⅝ times width of mouth. Rostral ridges rather narrow, separated throughout their length, parallel anteriorly, diverging a little posteriorly.

Diameter of eye $3\frac{1}{2}$ to 4 in præorbital length of snout, that of eye + spiracle $1\frac{1}{4}$ to $1\frac{2}{5}$ in distance between spiracles. Only the outer spiracular fold developed. Nostrils short, oblique, $1\frac{3}{4}$ to nearly twice in width of mouth, about equal to that of internarial space; anterior valve extending inwards well beyond level of inner edge of nostril, nearly meeting that of opposite side. Mouth nearly straight. First dorsal $1\frac{1}{2}$ to $1\frac{3}{4}$ times as high as long; origin a distance behind base of pelvics equal to or a little

Text-figure 21.



*Rhinobatus blochii.* (× $\frac{2}{5}$.)

greater or less than that between the two dorsals; base 2 to $2\frac{1}{3}$ in distance between dorsals. Skin covered with minute denticles, smooth to the touch; a series of small spines in the median line of the back, and some smaller ones on head and scapular region: all the spines becoming less prominent and irregularly disposed in older examples. Young with a few small, round white spots on upper surface of head and body.

*Hab.* South Africa.

| | | |
|---|---|---|
| 1-2. (♀, 945 & 960 mm.), stuffed. | Cape of Good Hope. | |
| 3. (♂, 385 mm ) | Cape of Good Hope. | |
| 4. (♂, 360 mm.). | Table Bay. | Gilchrist. |
| 5. (♀, 225 mm.). | Table Bay. | Gilchrist. |

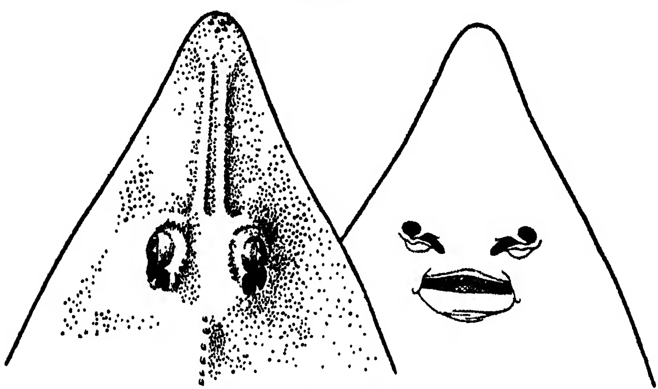
20. Rhinobatus lentiginosus.

*Rhinobatus lentiginosus* Garman, Bull. Mus. Comp. Zool. vi. 1880, p. 168; Proc. U.S. Nat. Mus. iii. 1881, p. 519; Jordan & Evermann, Bull. U.S. Nat. Mus. xlvii. 1896, p. 62, pl. viii. fig. 28, pl. ix. figs. 28 *a–b*; Garman, Mem. Mus. Comp. Zool. xxxvi. 1913, p. 279, pl. 17.

Snout rather long, bluntly pointed, the margins nearly straight; its præorbital length $2\frac{4}{5}$ times the distance between the spiracles, and its præoral length about 3 times width of mouth. Rostral ridges rather broad, narrowly separated throughout their length, nearly parallel. Diameter of eye 6 in præorbital length of snout, that of eye + spiracle a little less than distance between

spiracles. Both folds of spiracle developed, the outer the more prominent. Nostrils of moderate length, oblique, $1\frac{4}{5}$ in width of mouth, a little greater than that of internarial space; anterior valve scarcely extending inwards. Mouth nearly straight. First dorsal $1\frac{3}{5}$ times as high as long; origin a distance behind base of pelvics about equal to that between the two dorsals; base $2\frac{1}{3}$ in distance between dorsals. Skin covered with minute denticles,

Text-figure 22.



*Rhinobatus lentiginosus.* (× $\frac{1}{4}$.)

smooth to the touch; a series of rather small, blunt spines in the median line of the back, a single pair on each shoulder, and several spines round the orbits and above the spiracles; a small group of stronger spines above tip of snout. Back greyish, densely freckled with small paler spots.

*Hab.* Atlantic Coast of America from North Carolina southwards to the coast of Florida.

1. (♀, 780 mm.). Morehead, N.C. Coles.

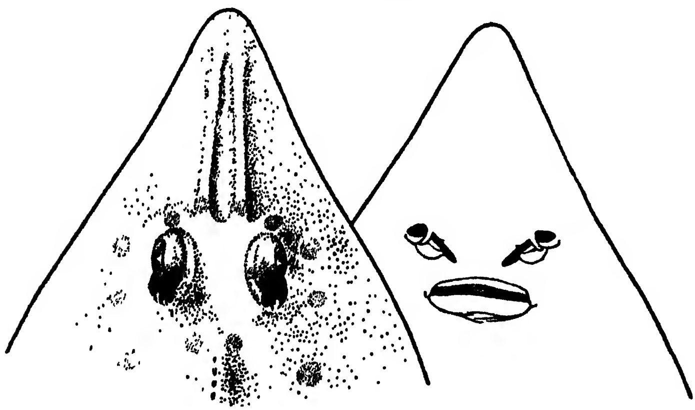
21. Rhinobatus glaucostigma.

*Rhinobatus glaucostigma* Jordan & Gilbert, Proc. U.S. Nat. Mus. vi. 1884, p. 210; Jordan & Evermann, Bull. U.S. Nat. Mus. xlvii. 1896, p. 62; Boulenger, Boll. Mus. Zool. Anat. Torino, xiii. 1898, no. 329, p. 1; Garman, Mem. Mus. Comp. Zool. xxxvi. 1913, p. 282.

Snout moderate, bluntly pointed, the margins nearly straight; its præorbital length $2\frac{2}{5}$ times the distance between the spiracles, and its præoral length nearly 3 times width of mouth. Rostral ridges rather broad, widely separated throughout their length, nearly parallel. Diameter of eye 6 in præorbital length of snout, that of eye + spiracle $\frac{5}{8}$ of distance between spiracles. Both folds of spiracle developed, the outer the more prominent.

Nostrils rather long, oblique, $1\frac{3}{5}$ in width of mouth, $1\frac{1}{3}$ times that of internarial space; anterior valve extending a little inwards. Mouth nearly straight. First dorsal nearly twice as high as long; origin a distance behind base of pelvics about equal to that between the two dorsals; base $2\frac{4}{5}$ in distance between dorsals. Skin covered with minute denticles, smooth to the

Text-figure 23.



*Rhinobatus glaucostigma.* (× $\frac{1}{3}$.)

touch; a series of small, blunt spines in the median line of the back, a single group on each shoulder, and several spines round the orbits and above the spiracles. Back brownish grey; a series of round slate-coloured spots symmetrically arranged; pectoral and pelvic fins with pale margins; a dark blotch and some irregular dark patches below the snout.

*Hab.* Pacific Coast of America from the Gulf of California to Ecuador.

| | | |
|---|---|---|
| 1. (♀, 580 mm.). | Mazatlan. | Jordan. |

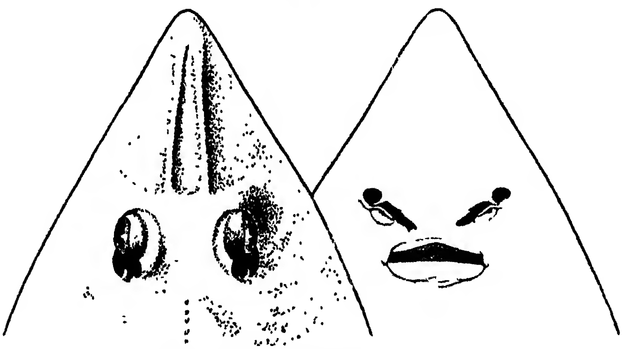
22. Rhinobatus leucorhynchus.

*Rhinobatus leucorhynchus* Günther, Proc. Zool. Soc. 1866, p. 604; Trans. Zool. Soc. vi. 1869, p. 490; Cat. Fish. viii. p. 444, fig. (1870); Garman, Proc. U.S. Nat. Mus. iii. 1881, p. 517; Jordan & Evermann, Bull. U.S. Nat. Mus. xlvii. 1896, p. 62; Gilbert & Starks, Mem. Calif. Acad. Sci. iv. 1904, p. 14; Garman, Mem. Mus. Comp. Zool. xxxvi. 1913, p. 282; Meek & Hildebrand, Pub. Field Mus. Nat. Hist., Zool. Ser. xv. 1923, p. 68.

Snout moderate, pointed, the margins straight; its præorbital length a little more than twice the distance between the spiracles, and its præoral length about $2\frac{3}{5}$ times width of mouth. Rostral

ridges narrow, widely separated throughout their length, converging anteriorly. Diameter of eye $4\frac{3}{4}$ to 5 in præorbital length of snout, that of eye + spiracle $\frac{3}{4}$ to $\frac{4}{5}$ of distance between spiracles. Both folds of spiracle developed, the outer the more prominent. Nostrils rather long, oblique, $1\frac{1}{2}$ in width of mouth, $1\frac{2}{5}$ to $1\frac{3}{5}$ times that of internarial space; anterior valve scarcely extending inwards. Mouth nearly straight. First dorsal $1\frac{3}{4}$ to

Text-figure 24.



*Rhinobatus leucorhynchus.* (× $\frac{1}{3}$.)

twice as high as long; origin a distance behind base of pelvics about equal to that between the two dorsals; base $2\frac{2}{3}$ to $2\frac{4}{5}$ in distance between dorsals. Skin covered with minute denticles, smooth to the touch; a series of small spines in the median line of the back, in two groups on each shoulder, and several spines round the orbits and above the spiracles.

*Hab.* Pacific Coast of Central America.

| | | |
|---|---|---|
| 1. (♂, 560 mm.). Type of the species. | Pacific Coast of Central America. | Dow. |
| 2. (♀, 625 mm.). | Panama. | Jordan. |

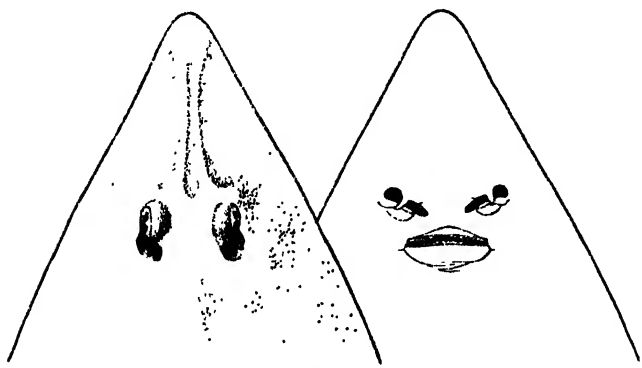
23. Rhinobatus stellio.

*Rhinobatus stellio* Jordan & Rutter, Proc. Acad. Nat. Sci. Philad. 1897, p. 91.

Snout moderate, pointed, the margins straight; its præorbital length nearly 3 times the distance between the spiracles, and its præoral length $2\frac{5}{6}$ times width of mouth. Rostral ridges rather narrow, narrowly separated anteriorly, diverging posteriorly. Diameter of eye $4\frac{1}{3}$ in præorbital length of snout, that of eye + spiracle nearly equal to distance between spiracles. Both folds of spiracle developed, the outer the more prominent. Nostrils of moderate length, oblique, $1\frac{3}{4}$ in width of mouth, a little greater than that of internarial space; anterior valve scarcely extending inwards. Mouth nearly straight. First dorsal about $1\frac{3}{4}$ times

as high as long; origin a distance behind base of pelvics about equal to that between the two dorsals; base $2\frac{1}{6}$ in distance between dorsals. Skin covered with minute denticles, smooth to the touch; a series of small, blunt spines in the median line of the back, a single minute spine on each shoulder, and several

Text-figure 25.



*Rhinobatus stellio.* (× ½.)

small ones round the orbits and above the spiracles. Back brownish; numerous small white spots, all smaller than the pupil, symmetrically arranged; edges of lower surface of snout stained with darker.

*Hab.* Jamaica.

| | | |
|---|---|---|
| 1. (♀, 295 mm.). | Jamaica. | Roberts. |

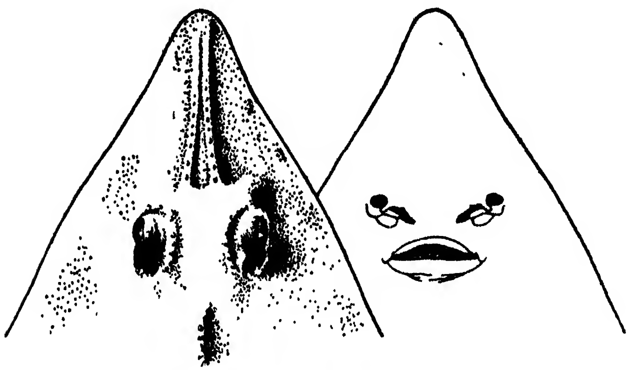
24. Rhinobatus productus.

*Rhinobatus productus* Girard, Proc. Acad. Nat. Sci. Philad. vii. 1856, p. 196; Garman, Proc. U.S. Nat. Mus. iii. 1881, p. 517; Jordan & Evermann, Bull. U.S. Nat. Mus. xlvii. 1896, p. 63; Starks & Morris, Univ. Calif. Pub. Zool. iii. 1907, p. 168; Garman, Mem. Mus. Comp. Zool. xxxvi. 1913, p. 281.

Snout moderate, bluntly pointed, the margins straight; its præorbital length $2\frac{1}{3}$ to $2\frac{1}{2}$ times the distance between the spiracles, and its præoral length $2\frac{2}{3}$ to 3 times width of mouth. Rostral ridges rather narrow, more or less approximated in the anterior half of their length, diverging posteriorly. Young of both sexes with a fringed membranous flap above the tip of the snout. Diameter of eye $4\frac{1}{3}$ to $5\frac{2}{3}$ in præorbital length of snout, that of eye + spiracle $\frac{4}{5}$ to $\frac{7}{8}$ of distance between spiracles. Both folds of spiracle developed, the outer the more prominent. Nostrils rather long, oblique, $1\frac{2}{3}$ to $1\frac{1}{4}$ in width of mouth, $1\frac{1}{4}$ to $1\frac{1}{8}$ times that of internarial space; anterior valve extending a

little inwards. Mouth nearly straight. First dorsal $1\frac{2}{3}$ to twice as high as long; origin a distance behind base of pelvics equal to or a little less than that between the two dorsals; base $2\frac{1}{4}$ to $2\frac{2}{3}$ in distance between dorsals. Skin covered with small or minute denticles; a series of strong, compressed spines in the median line of the back in the young, becoming blunter and more

Text-figure 26.



*Rhinobatus productus.* (× $\frac{1}{3}$.)

irregularly disposed with age; two spines on each shoulder, and several round the orbits and above the spiracles, which tend to become less prominent or to disappear almost entirely in the adults; young with a series of smaller spines on each rostral ridge. Sometimes a black blotch, or some irregular blackish markings below end of snout.

*Hab.* Coast of California.

| | | |
|---|---|---|
| 1–2. (♂, 850 & 880 mm.). | San Diego. | Eigenmann. |
| 3–5. (♂, ♀, 245–280 mm.). | San Diego. | Eigenmann. |
| 6. (♀, 350 mm.). | San Diego. | Smithsonian Institution. |
| 7–9. (♀, 350–700 mm.). | San Diego. | Jordan. |

25. Rhinobatus percellens.

*Raja percellens* Walbaum, Artedi Pisc. p. 525 (1792).

*Rhinobatus electricus* Bloch, Schneider, Syst. Ichth. p. 356 (1801).

*Rhinobatus undulatus* Olfers, Die Gattung *Torpedo*, p. 22 (1831); Günther, Cat. Fish. viii. p. 444 (1870); Garman, Proc. U.S. Nat. Mus. iii. 1881, p. 518.

*Rhinobatus glaucostictus* Olfers, *t. c.* p. 22 (1831).

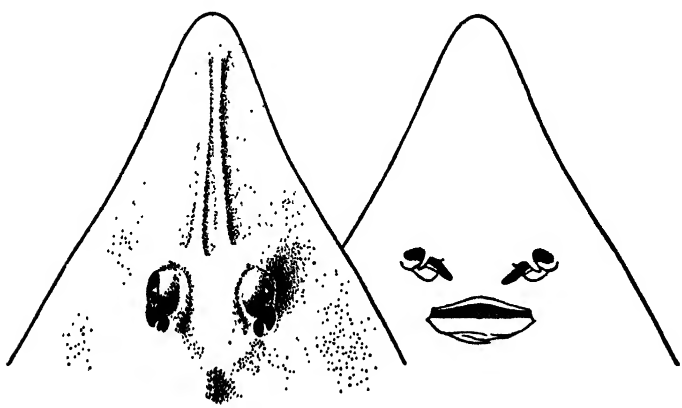
*Rhinobatus marcgravii* Henle, Ueber Narcine, p. 34 (1834).

*Rhinobatus (Rhinobatus) undulatus* Müller & Henle, Plagiost. p. 121, pl. 40 (1841); Duméril, Elasmobr. p. 498 (1865).

*Rhinobatus percellens* Jordan & Evermann, Bull. U.S. Nat. Mus. xlvii, 1896, p. 63; Garman, Mem. Mus. Comp. Zool. xxxvi. 1913, p. 278, pl. 55. fig. 4, pl. 56. fig. 7, pl. 65. fig. 2; Starks, Fishes Stanford Exped. Brazil, p. 5 (1913); Ribeiro, Fauna Brasiliense, Peixes, ii. pt. 1, fasc. 1 Desmobr. p. 31, pl. xi. (1923); Meek & Hildebrand, Pub. Field Mus. Nat. Hist., Zool. Ser. xv. 1923, p. 69.

Snout rather long, bluntly pointed, the margins scarcely concave; its præorbital length $2\frac{5}{8}$ to 3 times the distance between the spiracles, and its præoral length $2\frac{3}{4}$ to 3 times width of mouth. Rostral ridges rather narrow, close together and parallel for a little more than half their length, diverging posteriorly; more or less expanded near extremity of snout. Diameter of eye $4\frac{4}{5}$ to 6 in præorbital length of snout, that of eye + spiracle about $\frac{5}{8}$ of distance between spiracles. Space between orbital ridges concave, its width $4\frac{2}{3}$ to 5 in præorbital length of snout. Both folds of spiracle developed, the outer the

Text-figure 27.



*Rhinobatus percellens.* (× $\frac{1}{3}$.)

more prominent. Nostrils of moderate length, oblique, $1\frac{4}{5}$ to nearly twice in width of mouth, a little greater than that of internarial space; anterior valve extending a little inwards. Mouth nearly straight. First dorsal $1\frac{3}{4}$ times as high as long; origin a distance behind base of pelvics a little greater than that between the two dorsals; base $2\frac{1}{4}$ to $2\frac{4}{5}$ in distance between dorsals. Skin covered with minute denticles, smooth to the touch; a series of small, rather blunt spines in the median line of the back, one or two inconspicuous spines on each shoulder, and several small ones round the orbits and above the spiracles. Back greyish brown, generally with some indistinct darker

markings on body, and some faint irregular bars across the upper surface of the tail; sometimes a dark blotch and other markings below the snout.

*Hab.* West Indies to the Rio Plata.

| | | |
|---|---|---|
| 1. (♂, 300 mm.). | Bahia. | Wucherer. |
| 2. (♀, 600 mm.). | Rio de Janeiro. | Ternetz. |

In addition to the above specimens, on which my description is based, a stuffed example (♀, 485 mm.) probably belongs to this species.

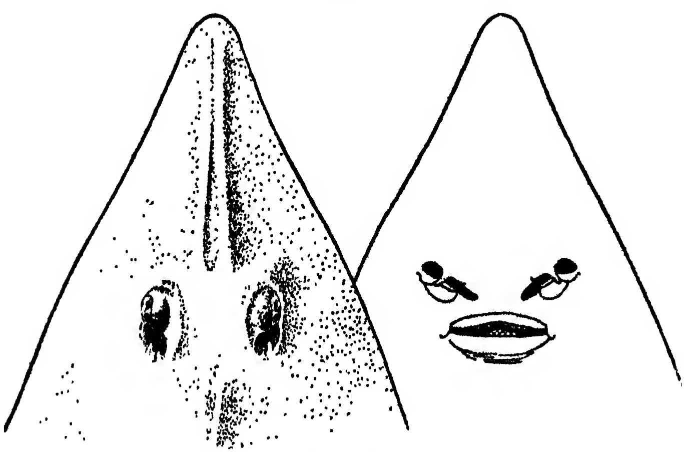
26. Rhinobatus horkelii.

*Rhinobatus* (*Rhinobatus*) *horkelii* Müller & Henle, Plagiost. p. 122, pl. 41 (1841); Duméril, Elasmobr. p. 499 (1865).

*Rhinobatus horkelii* Garman, Proc. U.S. Nat. Mus. iii. 1881, p. 518; Mem. Mus. Comp. Zool. xxxvi. 1913, p. 280; Ribeiro, Fauna Brasiliense, Peixes, ii. pt. i. fasc. 1 Desmobr. p. 31 (1923).

Perhaps not distinct from the preceding species. Præorbital length of snout about 3 times the distance between the spiracles, præoral length a little more than 3 times width of mouth.

Text-figure 28.



*Rhinobatus horkelii.* (× ½.)

Rostral ridges somewhat broader than in *R. percellens.* Diameter of eye 8 in præorbital length of snout, that of eye + spiracle ⅘ of distance between spiracles. Space between orbital ridges flat, its width 4½ in præorbital length of snout. Nostrils longer than in *R. percellens*, 1½ in width of mouth, nearly 1½ times that

of internarial space. Spines in the median line of the back more prominent. Coloration uniform.

*Hab.* Coast of Brazil.

1. (♂, 900 mm.). Rio de Janeiro. Goldi.

A young example (♀, 225 mm.) from Rio Grande do Sul probably belongs to this species.

27. Rhinobatus planiceps.

*Rhinobatus planiceps* Garman, Bull. Mus. Comp. Zool. vi. 1880, p. 168; Proc. U.S. Nat. Mus. iii. 1881, p. 520; Bull. Mus. Comp. Zool. xvii. 1888, p. 89, pl. xxiv.; Jordan & Evermann, Bull. U.S. Nat. Mus. xlvii. 1896, p. 64; Garman, Mem. Mus. Comp. Zool. xxxvi. 1913, p. 283.

Snout moderate, bluntly pointed, the margins straight; its præorbital length a little more than twice the distance between the spiracles, and its præoral length about $2\frac{3}{5}$ times width of mouth. Rostral ridges rather narrow, parallel and close together anteriorly, diverging posteriorly. Diameter of eye nearly 4 times in præorbital length of snout, that of eye + spiracle a little less than distance between spiracles. Spiracle with a single rudimentary fold. Nostrils of moderate length, oblique, $1\frac{2}{3}$ in width of mouth, $1\frac{1}{3}$ times that of internarial space; anterior valve scarcely extending inwards. Base of first dorsal nearly twice its length from second dorsal, and from base of pelvics. A series of small tubercles in the median line of the back, in two groups on each shoulder, and several round the orbits and spiracles; very young examples with a series of spines above each rostral ridge; in old examples all the tubercles are relatively smaller. Brownish, with or without small white spots on the back, symmetrically arranged; sometimes a black blotch below the end of the snout.

*Hab.* Peru to the Galapagos Islands.

The above description is based partly on Garman's descriptions of the species, and partly on measurements made from his figures.

## 4. Aptychotrema, gen. nov.

Close to *Rhinobatus*, differing in the almost transverse nostrils, with the inward extension of the anterior nasal valve crossing the inner angle of the nostril, and in the absence of spiracular folds.

Two species from Australia.

### *Synopsis of the Species.*

I. Præorbital length of snout nearly 3 times distance between spiracles, præoral length $2\frac{4}{5}$ times width of mouth; mouth strongly curved; teeth in the middle of the lower jaw enlarged; horizontal distance from outer edge of nostril to lateral margin of snout about 5 in præoral length of snout........................................ 1. *bougainvillii.*

II. Præorbital length of snout $3\frac{3}{8}$ times distance between spiracles, præoral length $3\frac{1}{4}$ times width of mouth; mouth slightly curved; teeth all of the same size; horizontal distance from outer edge of nostril to lateral margin of snout about $4\frac{2}{3}$ in præoral length of snout .................... 2. *banksii*.

In general form the two species of this genus resemble *Rhinobatus granulatus*, in which the nostrils are more transverse than in any other member of that genus. In *Rhinobatus granulatus*, however, the inward extension of the anterior nasal valve terminates near the middle of the anterior margin of the nostril, and the outer spiracular fold, although feebly developed, is quite distinct.

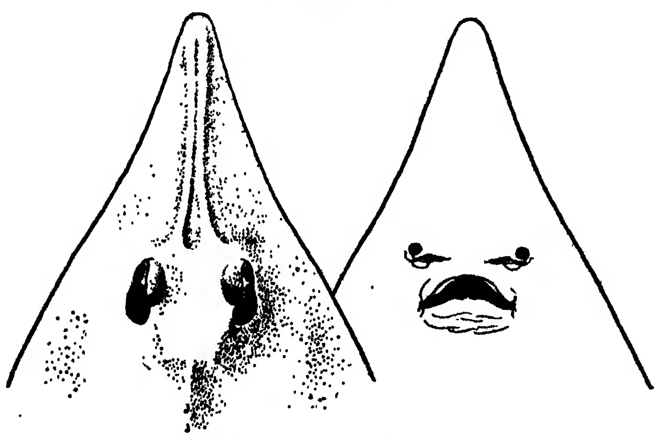
1. Aptychotrema bougainvillii.

*Rhinobatus* (*Syrrhina*) *bougainvillii* (Val.), Müller & Henle, Plagiost. p. 117 (1841); Duméril, Elasmobr. p. 491, pl. 10. fig. 1 (1865).

*Rhinobatus bougainvillii* Günther, Cat. Fish. viii. p. 445 (1870); Ogilby, Proc. Linn. Soc. N. S. Wales, x. 1886, p. 464; Garman, Mem. Mus. Comp. Zool. xxxvi. 1913, p. 277.

*Hab.* Coast of New South Wales *.

Text-figure 29.



*Aptychotrema bougainvillii.* (×

In the British Museum a single specimen (♂), 825 mm. in total length, from Port Jackson.

2. Aptychotrema banksii.

*Rhinobatus* (*Rhinobatus*) *banksii* Müller & Henle, Plagiost. p. 123 (1841).

* The type-locality of this species is unknown.

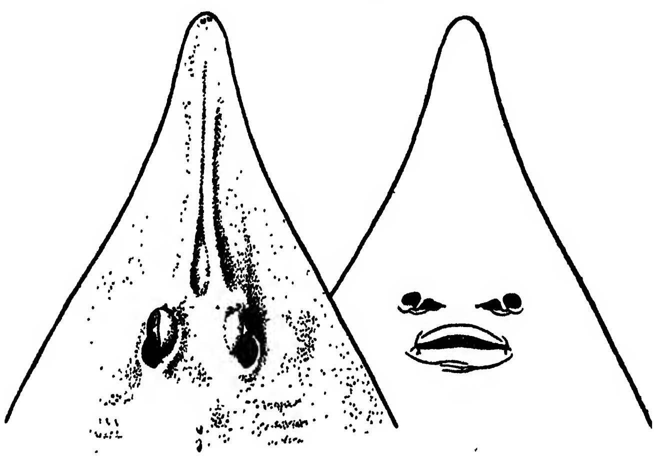
*Rhinobatus* (*Syrrhina*) *banksii* Müller & Henle, *t.c.* p. 192 (1841); Duméril, Elasmobr. p. 490 (1865).

*Rhinobatus banksii* Günther, Cat. Fish. viii. p. 446 (1870); Macleay, Proc. Linn. Soc. N.S. Wales. vi. 1882, p. 372; Waite, Mem. Austral. Mus. iv. 1899, p. 38, pl. iii.; Ogilby, Mem. Queensland Mus. v. 1916, p. 85, fig. 1; McCulloch & Whitley, *ibid.* viii. 1925, p. 129.

*Rhinobatus vincentianus* Haacke, Zool. Anz. viii. 1885, p. 508.

*Rhinobatus philippi* Garman, Mem. Mus. Comp. Zool. xxxvi. 1913, p. 278; Waite, Rec. S. Austral. Mus. ii. 1921, p. 27 fig. 38.

Text-figure 30.



*Aptychotrema banksii.* (× ⅜)

*Hab.* Southern Australia northwards to Southern Queensland.

In the British Museum a single specimen (♂), 455 mm. in total length, from Botany Bay, New South Wales ('Endeavour' collection).

The two species of *Aptychotrema* appear to have been sometimes confused by Australian ichthyologists. Some of the records of *banksii* probably refer to *bougainvillii*.

## 5. Zapteryx.

*Syrrhina* (part.) Müller & Henle, Plagiost. p. 113 (1841).

*Rhinobatus* (part.) Günther, Cat. Fish. viii. p. 441 (1870).

*Zapteryx* Jordan & Gilbert, Proc. U.S. Nat. Mus. iii. 1881, p. 53.

*Syrrhina* Garman, Proc. U.S. Nat. Mus. iii. 1881, p. 520; Mem. Mus. Comp. Zool. xxxvi. 1913, p. 284.

Two or three species from the coasts of tropical America.

### *Synopsis of the Species.*

I. Rostral ridges converging anteriorly; one spiracular fold; origin of first dorsal a distance behind base of pelvics $1\frac{3}{4}$ to twice that between the two dorsals; back uniformly coloured or clouded with brown .. ....... .... 1. *brevirostris*.

II. Rostral ridges nearly parallel, scarcely converging anteriorly; spiracular fold rudimentary or absent; origin of first dorsal a distance behind base of pelvics $1\frac{1}{3}$ to $1\frac{1}{4}$ times that between the two dorsals; back with transverse bands or ocellated spots.

A. Disc a little longer than broad; back without yellow spots. 2. *exasperata*.

B. Disc a little broader than long; back with black-edged yellow spots ... . . . . ......... ...... 3. *xyster*.

1. Zapteryx brevirostris.

*Rhinobatus* (*Syrrhina*) *brevirostris* Müller & Henle, Plagiost. p. 114, pl. 36 (1841); Duméril, Elasmobr. p. 489 (1865).

*Rhinobatus brevirostris* Günther, Cat. Fish. viii. p. 447 (1870); Ribeiro, Fauna Brasiliense, Peixes, ii. pt. 1, fasc. 1 Desmobr. p. 31, pl. xii. (1923).

*Syrrhina brevirostris* Garman, Bull. Mus. Comp. Zool. xvii. 1888, p. 89, pl. xxv.; Mem. Mus. Comp. Zool. xxxvi. 1913, p. 285, pl. 65. fig. 3.

*Hab.* Coast of Brazil.

In the British Museum three specimens, 410 to 450 mm. in total length, including one of the types of the species.

2. Zapteryx exasperata.

*Trigonorhina exasperata* Garman, Bull. Mus. Comp. Zool. vi. 1880, p. 170.

*Trigonorhina alveata* Garman, *t. c.* p. 169.

*Platyrhina exasperata* Jordan & Gilbert, Proc. U.S. Nat. Mus. iii. (1880) 1881, p. 32.

*Zapteryx exasperata* Jordan & Gilbert, *t. c.* p. 53; Jordan & Evermann, Bull. U.S. Nat. Mus. xlvii. 1896, p. 64.

*Syrrhina exasperata* Garman, Proc. U.S. Nat. Mus. iii. (1880) 1881, p. 521; Mem. Mus. Comp. Zool. xxxvi. 1913, p. 286.

*Rhinobatus exasperatus* Jordan & Gilbert, Bull. U.S. Nat. Mus. xvi. 1882, p. 63.

*Hab.* San Diego, California.

In the British Museum two specimens, 175 and 185 mm. in total length.

3. Zapteryx xyster.

*Syrrhina exasperata* Jordan & Gilbert, Proc. U.S. Nat. Mus. v. 1883, p. 621.

*Zapteryx xyster* Jordan & Evermann, Bull. U.S. Nat. Mus. xlvii. 1896, p. 65.

*Syrrhina xyster* Garman, Mem. Mus. Comp. Zool. xxxvi. 1913, p. 286.

*Hab.* Panama.

This species, known only from the types (♀, 22 inches), may not be distinct from *Z. exasperatus.*

### 6. Trygonorhina.

*Trygonorrhina* Müller & Henle, Mag. Nat. Hist. n. s. ii. 1838, p. 90.

*Trygonorhina* Müller & Henle, Plagiost. p. 124 (1841); Günther, Cat. Fish. viii. p. 447 (1870); Garman, Mem. Mus. Comp. Zool. xxxvi. 1913, p. 287.

A single species from Australia.

#### 1. Trygonorhina fasciata.

*Trygonorhina fasciata* Müller & Henle, Plagiost. p. 124, pl. 43 (1841); Duméril, Elasmobr. p. 502 (1865); Günther, Cat. Fish. viii. p. 448 (1870); McCulloch, Proc. Linn. Soc. N. S. Wales, xlvi. 1921, p. 460, pl. xxxviii. figs. 1-2.

*Trygonorrhina fasciata* Garman, Mem. Mus. Comp. Zool. xxxvi. 1913, p. 287.

*Hab.* Australia; Tasmania.

In the British Museum thirteen specimens, 300 to 860 mm. in total length.

### 7. Platyrhinoidis.

*Platyrhinoidis* Garman, Proc. U.S. Nat. Mus. iii. (1880) 1881, p. 522; Mem. Mus. Comp. Zool. xxxvi. 1913, p. 290.

A single species from California.

#### 1. Platyrhinoidis triseriata.

*Platyrhina triseriata* Jordan & Gilbert, Proc. U.S. Nat. Mus. iii. 1881, p. 36.

*Platyrhinoidis triseriata* Garman, Proc. U.S. Nat. Mus. iii. 1881, p. 522; Jordan & Evermann, Bull. U.S. Nat. Mus. xlvii. 1896, p. 65; Garman, Mem. Mus. Comp. Zool. xxxvi. 1913, p. 290.

*Rhinobatus triseriatus* Jordan & Gilbert, Bull. U.S. Nat. Mus. xvi. 1882, p. 64.

*Hab.* Coast of California.

In the British Museum a single specimen (♀), 540 mm. in total length.

### 8. Zanobatus.

*Zanobatus* Garman, Mem. Mus. Comp. Zool. xxxvi. 1913, p. 291.

A single species.

1. ZANOBATUS SCHŒNLEINII.

*Platyrhina schœnleinii* Müller & Henle, Plagiost. p. 125, pl. 45 (1841); Duméril, Elasmobr. p. 577 (1865); Günther, Cat. Fish. viii. p. 471 (1870): Steindachner, Denkschr. Akad. Wien, xliv. 1882, p. 50, pl. vii.

*Discobatus schœnleinii* Garman, Proc. U.S. Nat. Mus. iii. 1881, p. 523.

*Zanobatus schœnleinii* Garman, Mem. Mus. Comp. Zool. xxxvi. 1913, p. 291.

*Hab.* West Africa; India.

In the British Museum a single specimen (♀), 170 mm. in total length, from Lagos.

As far as I am able to judge from a partial dissection of this very young example, the rostral cartilage does not reach the extremity of the snout in this species; this point, however, requires confirmation.

9. PLATYRHINA.

*Platyrhina** Müller & Henle, Mag. Nat. Hist. n. s. ii. 1838, p. 90; Plagiost. p. 125 (1841).

*Analithis* Gistl, Nat. Thierr. p. x (1848).

*Platyrhina* (part.) Günther, Cat. Fish. viii. p. 470 (1870).

*Discobatus* Garman, Proc. U.S. Nat. Mus. iii. 1881, p. 523; Mem. Mus. Comp. Zool. xxxvi. 1913, p. 288.

A single species from China and Japan.

1. PLATYRHINA SINENSIS.

*La raie chinoise* Lacepède, Hist. Nat. Poissons, i. p. 157, pl. ii. fig. 2 (1798).

*Rhina sinensis* Bloch, Schneider, Syst. Ichth. p. 352 (1801).

*Platyrhina sinensis* Müller & Henle, Plagiost. p. 125, pl. 44 (1841); Duméril, Elasmobr. p. 576 (1865); Günther, Cat. Fish. viii. p. 471 (1870).

*Discobatus sinensis* Garman, Proc. U.S. Nat. Mus. iii. 1881, p. 523; Jordan & Fowler, *ibid.* xxvi. 1903, p. 647; Garman, Mem. Mus. Comp. Zool. xxxvi. 1913, p. 289.

*Hab.* Coasts of China and Japan.

In the British Museum four specimens, 160 to 450 mm. in total length.

* Not *Platyrhinus* Schellenberg—a genus of Coleoptera.

# 49. The Function of the "Funnel" Mouth of the Tadpoles of *Megalophrys*, with a Note on *M. aceras* Boulenger.

By MALCOLM A. SMITH, M.R.C.S., L.R.C.P., F.Z.S.

[Received May 27, 1926: Read November 2, 1926.]

(Text-figures 1, 2.)

It has long been known that the tadpoles of the genus *Megalophrys* can be separated into two sharply defined groups: namely, those with horny mandibles and teeth of the ranid type, and those which are toothless but in which the lips have been enlarged and modified to form a funnel. Of the tadpoles of the latter type we are now acquainted with some six or seven species, whilst of the former only two, and it is interesting to find, in so far as our knowledge at present extends, that the two types of tadpoles develop into the two sharply defined groups which characterize the adults: namely, those in which the snout projects strongly beyond the mouth, and those in which it does not. The tadpoles with the "funnel" mouth belong to the first named group.

The precise function or functions of the "funnel" mouth of these tadpoles is still contested by various observers, and I do not propose here to enter into all the views that have been advanced. I should like, however, to discuss some of those that have been more recently put forward *. In 1917, after a week's observation of these larvæ in their native habitat, followed by four months almost daily observation of them in captivity, I proposed the view that the chief, if not the sole, purpose of this apparatus was to enable the creature to obtain its food. This was drawn from the surface of the water, the function of the "funnel" being to furnish as large an area as possible for collecting minute particles floating upon the surface of the water which were drawn towards it by suction. My observations at that time were made upon the larvæ of *Megalophrys major*; since then I have had further experiences with those of *M. aceras* in southern Siam and *M. montana* in Java.

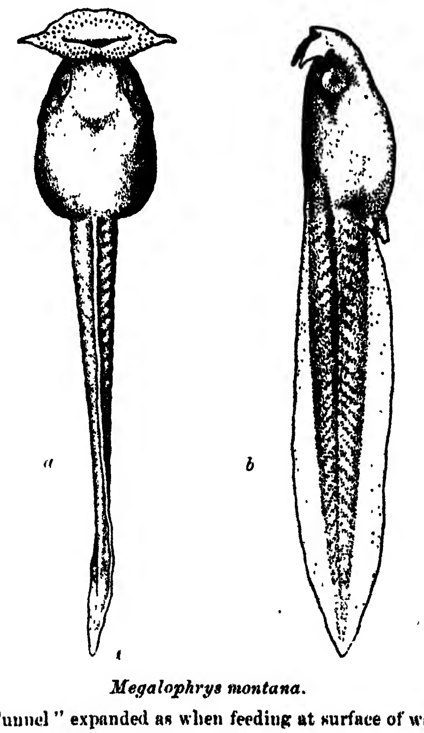
A tadpole belonging to an entirely different family of Amphibians, namely the brevicipitid *Microhyla achatina* †, has developed

* "The Funnel Apparatus of the Larvæ of *Megalophrys montana*," by Dr. H. Boschma, Bijdr. Dierkunde Amsterdam (Max Weber Feest-nummer), xxii. pp. 9–12 (1922). "Some Observations on the Oral Apparatus of the Tadpoles of *Megalophrys parva*," by Sunder Lal Hora, M.Sc., Journ. & Proc. Asiat. Soc. Bengal, xviii. pp. 9–15 (1922). "Observations on the Fauna of Certain Torrential Streams in the Khasi Hills," by Sunder Lal Hora, D.Sc., Rec. Ind. Mus. xxv. pp. 579–600 (1923).

† Described in Journ. Nat. Hist. Soc. Siam, 1916, ii. p. 37, fig.

a mouth not unlike that of the *Megalophrys* larvæ, but whereas in *M. achatina* only the lower lip has become enlarged, in *Megalophrys* both lips have become hypertrophied, so that a cup-shaped orifice results with the true mouth at the bottom of it. The majority of the brevicipitid larvæ that I am acquainted with (*Microhyla* spp., *Glyphoglossus*, *Calluella*), derive their nourishment from minute atoms in the water. They are never seen definitely to eat anything, but pass their days

Text-figure 1.




*Megalophrys montana.*

*a.* "Funnel" expanded as when feeding at surface of water.
*b.* "Funnel" folded when at rest.

endlessly floating about, often in vast congregations, a short distance below the surface of the water, continually imbibing it and drawing their nourishment from it. *M. achatina* is an exception to this. That it derives some of its nourishment from the body of the water, as do the other members of its genus, is most likely, but that its main supply is drawn from the surface of the water, and that the lower lip has become specially enlarged and adapted to enable it to do this, can

hardly be doubted by anyone who has kept and watched these creatures. They can be seen continually rising to the surface and sucking in the tiny particles of matter which may be floating there; if they are lying below it and fragments of vegetable dust are dropped on the water above them, they at once rise up and devour them, elevating the lower lip as they reach the surface and by vigorous suction drawing them into the mouth from all sides.

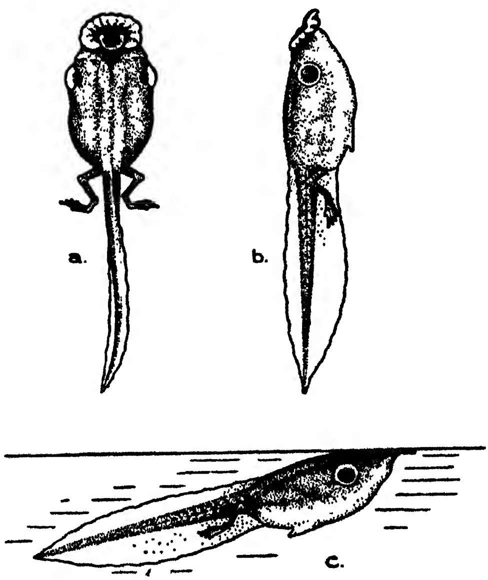
Other tadpoles, both of the ranid and brevicipitid type, can be seen at times "nibbling" the surface of the water, presumably for nourishment, but they have no special adaptation of the mouth for feeding in this manner.

It was the discovery of the mode of feeding by the tadpole of *M. achatina*, that first led me to infer a similar use for the "funnel" mouth of the larva of *Megalophrys*. Upon this point Hora states "it does not appear to me likely that the animal in its natural habitat comes to the surface and expands its funnel for feeding purposes, for I believe that in nature, as under artificial conditions, the tadpole spends most of its time under water with the funnel folded." My own experience is so entirely the reverse of this that I am led to doubt if Professor Hora has really discovered the conditions under which these larvæ prefer to feed. Although they may be found in the deeper pools of the streams they inhabit, it is in the shallowest puddles, among thick vegetation, that they are to be seen generally feeding. My captive specimens were in a large bath, and to imitate their natural surroundings as closely as possible, I provided them with several bricks upon which the water lay scarcely a centimetre deep. Here amongst water-weed they spent most of their time, with the body resting upon a brick and parallel with the surface of the water, and in this situation they were to be seen constantly feeding. This horizontal position is impossible in deeper water, where, when hanging from the surface, the body drops almost vertically or at an angle of about 45 degrees.

The corrugations upon the lip of *Microhyla achatina* are so similar, both in arrangement and structure, to the so-called "teeth" on the funnel of *Megalophrys*, that it is difficult to resist the conclusion that they have been evolved for the same purpose. In *Microhyla* they are simply ridges which are soft to the touch, whilst in *Megalophrys* they have become more specialized and are split up into a number of horny projections which are quite rough to the touch. In both, however, they are arranged in the same way, which is in a series of lines converging from the periphery of the lip towards the orifice of the true mouth. When first studying these corrugations to find a reason for their presence I believed they were made to serve as filters, for in watching the larvæ feed it was noticed that all large particles of matter were obstructed by them and thus prevented from entering the mouth, until ultimately,

when several pieces had accumulated, they were spat forcibly away and so rejected. That these corrugations are useful in this way is obvious, but I am inclined now to think that their true function is to make the lips a more effective instrument in feeding. When the creature rises to the top of the water and unfolds its "funnel," some part or parts of this apparatus must break the surface film and form contact with the air. If the lips were smooth the tendency would be for the edge of

Text-figure 2.




*Microhyla achatina.*

*a.* Lip elevated for feeding. *b.* Lip lowered when not feeding.
*c.* Attitude when feeding at surface of the water.

the funnel to perform this service, and all particles floating upon the water would then be stopped at the periphery of the organ and prevented from entering the mouth. With the corrugations present to break the surface, the edge of the lip can be kept just below it and the water is then sucked in through the channels thus formed. In *M. achatina* it can be seen that the edge of the lip is bent slightly downwards so as not to

interfere with the flow of water which is drawn from the sides and in front. The water directly above the head of the creature is prevented from entering by the curved upper lip, which breaking the surface of the water at that point forms an effective barrier to its entrance there.

Most authors are of the opinion that the funnel performs two or even three entirely different functions. It seems highly improbable, however, that so highly specialized a structure can have been evolved for more than one particular purpose; and any others it may at times perform are merely incidental ones. It is now generally agreed by recent observers that the "teeth" are neither used for grinding particles of food nor for rasping nourishment from the surfaces of leaves, although they may feed by suction from the under surface of leaves as I have seen the larvæ of *M. achatina* do. The creature, therefore, must take its food either from the body of the water as the brevicipitid larvæ do, or from the surface of the water by suction, for they have never been seen to feed in any other manner. Dr. Boschma's analysis of the intestinal contents shows that their food might have come from either of these two positions.

That the funnel can be used as a float is obvious, but I regard its power of floating as incidental to its hanging at the surface of the water to enable it to obtain its food. Dr. Annandale believed that unless the funnel was expanded the creature could not float, and that the very action of folding the funnel caused the creature to sink. Hora on the contrary states that he found the larvæ capable of floating irrespective of the fact that the funnel was expanded or folded. All of the brevicipitid larvæ that I am acquainted with, however,—*Kaloula pulchra* excepted—have the power of remaining suspended at any depth they like in the water. There is certainly a very close connection between the unfolding of the funnel and hanging by it from the surface of the water, while the fact that the creature has never been seen below the surface of the water with its lips unfolded suggests that the function of the funnel is connected with the surface of the water and with that only.

*Megalophrys aceras* mentioned earlier in this article was originally described by Boulenger as a varietal form of *M. montana*. I now believe it to be a distinct species. It differs in the narrower head (once and one-third times as broad as long), the larger and more distinct tympanum, the feebler web to the toes (never more than a rudiment), the dermal ridge beneath the fingers and toes, and in the disposition of the glandular folds upon the back. These last are very distinctive and separate it at once from *M. montana* and *M. nasuta*, two closely allied forms in which the folds run more or less straight

down the back. *M. aceras* with its V-shaped folds has evidently affinities with *M. major* and *M. longipes*, from both of which, however, it is distinct. Boulenger's figure of *M. aceras* in Fascic. Malay. Zool. 1903, i. p. 131, pl. v. is an excellent one.

I found this Toad common in the Nakon Sritamarat Mountains, S. Siam, at between 500 to 1000 metres altitude. Its habits were strictly nocturnal, and it could only be caught by hunting along the streams after nightfall with a lantern. During the day it could be sometimes heard, croaking dismally, but so deeply concealed in holes and clefts formed by the rocks that it was impossible to reach it. The separation of *M. aceras* from *M. montana* restricts the distribution of *montana* to the Malay Archipelago. I have examined all the specimens recorded as *montana* from the Malay Peninsula (Perak and Patani) and refer them to *M. aceras*.

Measurements of some specimens of *M. aceras* in mm. :—

| | | | | | | |
|---|---|---|---|---|---|---|
| Snout to vent ...... | 83 | 75 | 57 | 55 | 57 | 49 |
| Length of head ...... | 25 | 23 | 21 | 19 | 21 | 18 |
| Breadth of head ...... | 34 | 33 | 26 | 23 | 25 | 22 |
| Leg .................... | 119 | 98 | 84 | 78 | 85 | 78 |
| Tibia .................. | 35 | 32 | 28 | 26 | 28 | 26 |
| Hand .................. | 20 | 18 | 15 | 14 | 16 | 14 |
| Foot .................. | 32 | 28 | 23 | 22 | 22 | 22 |
| Author's no. ......... | 6129 | 1613 | 6131 | 6130 | 6132 | 6128 |
| | ♀ | ♀ | ♂ | ♂ | ♂ | ♂ |

# 50. Étude sur les Cavités Nasales des Carnassiers.

Par Dr. R. L. F. ANTHONY, C.M.Z.S., Professeur au Muséum national d'Histoire naturelle, Paris, et G. M. ILIESCO, Chef de travaux à la Faculté de Médecine Vétérinaire de Bucarest.

(Travail du laboratoire d'Anatomie comparée du Muséum national d'Histoire naturelle, Paris.)

[Received May 26, 1926: Read October 19, 1926.]

(Text-figures 1–9.)

SOMMAIRE



## PRÉLIMINAIRES.

En ces dernières années de nombreuses recherches ont été faites au laboratoire d'Anatomie comparée du Muséum national d'Histoire naturelle sur les cavités nasales des Mammifères.

M. R. Anthony et Mlle F. Coupin ont étudié celles de l'Eléphant *, puis celles de l'Okapi †, ce qui les a conduits à préciser la morphologie de celles des Ruminants en général.

A l'aide des matériaux du laboratoire, MM. M. Kollmann et L. Papin ont décrit celles des Lémuriens ‡.

M. R. Anthony doit bientôt donner la description de celles des Ongulés périssodactyles et Mlle F. Coupin la description de celles de l'Oryctérope §.

Tout récemment, l'un de nous, G. M. Iliesco ||, vient de publier

* R. Anthony et F. Coupin. Nouvelles recherches sur les cavités nasales de l'Eléphant d'Asie. Archives d'Anatomie, d'Histologie et d'Embryologie, Tome iv. 1925, pp. 107–147.

† R. Anthony et F. Coupin. Recherches anatomiques sur l'Okapi. Les sinus et les cornets nasaux. Revue zoologique africaine, vol. xiii. Fasc. i. 1925.

‡ M. Kollmann et L. Papin. Études sur les Lémuriens. Anatomie comparée des fosses nasales et de leurs annexes. Arch. de Morphologie génér. et expér. 1925, Fasc. 22.

§ Dans les Archives du Museum.

|| G. M. Iliesco. Recherches anatomiques sur les cavités nasales chez le Chat. Arch. d'Anatomie, d'Histologie et d'Embryologie. Tome v. 1925, pp. 1–48.

l'étude très détaillée des cavités nasales du Chat; les résultats de ses recherches sur celles du Chien paraîtront très prochainement *.

C'est pour compléter ces investigations que nous avons écrit le présent mémoire où la morphologie des cavités nasales est envisagée dans l'ensemble des Carnassiers, tant pinnipèdes que fissipèdes. S'ajoutant à ceux déjà parus, ou sur le point de paraître, il contribuera à fournir les éléments d'une synthèse qui jusqu'ici n'a pas pu être faite de l'Anatomie des cavités nasales dans l'ensemble des Mammifères.

Voici l'énumération des animaux que nous avons utilisés pour les présentes recherches :—

1°. *Fissipèdes.*

VIVERRIDÉS.
1. *Viverra civetta* Schreb. No. 1909-15 †.
2. *Viverra civetta* Schreb., ♂. No. 1923-489 (avec les parties molles).
3. *Viverra indica* Desm. No. 1926-79.
4. *Paradoxurus* sp.? No. 1909-35.

FÉLIDÉS.
5. *Felis leo* L., du Sénégal, ♂. No. 1926-80 (avec les parties molles).
6. *Felis leo* L., ♀ (jeune). No. 1898-295. (1.)
7. *Felis leo* L., ♀ (jeune). No. 1898-295. (2.)
8. *Felis leo* L., ♀. No. 1918-35.
9. *Felis tigris* L. No. 1889-408.
10. *Felis pardus* L. No. 1923-2444.
11. *Cynailurus jubatus* Erxleb., ♂. No. 1921-142.

HYÆNIDÉS.
12. *Hyæna striata* L., ♂. No. 1899-337.
13. *Hyæna crocuta* Zimm., ♂. No. 1926-15 (avec les parties molles).

URSIDÉS.
14. *Ursus arctos* L., ♂. No. 1918-40.
15. *Ursus arctos* L. de l'Ile Sakhaline. No. 1900-76.
16. *Ursus arctos* L., âgé de 20 j., ♂. No. 1921-4 (avec les parties molles).
17. *Ursus isabellinus* Horsf. (var. *syriacus* Hempr. et Ehrenb.) du Caucase. No. 1905-218.
18. *Ursus maritimus* Desm. du Spitzberg. No. 1869-71.
19. *Ursus ornatus* F. Cuv., ♀. No. 1848-369.

MUSTÉLIDÉS.
20. *Meles taxus* Bodd., ♀. No. 1905-111.
21. *Meles taxus* Bodd. No. 1900-386.
22. *Meles taxus* Bodd. No. 1901-626.
23. *Meles taxus* Bodd., ♀. No. 1907-125.
24. *Meles taxus* Bodd., ♂. No. 1916-107 (avec les parties molles).
25. *Lutra vulgaris* Erxl. No. 1893-522.
26. *Lutra vulgaris* Erxl., ♀. No. 1926-81.

PROCYONIDÉS.
27. *Procyon lotor* L. 1926-82.
28. *Nasua narica* L. (var. *fusca* Tomes), ♀. No. 1923-2400 (avec les parties molles).
29. *Nasua rufa* Desm. No. 1926-107.

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* Dans les Archives d'Anatomie, d'Histologie et d'Embryologie.

† Ces numéros se rapportent aux réserves d'études du service d'Anatomie comparée du Muséum national d'Histoire naturelle.

2°. *Pinnipèdes.*

| | |
|---|---|
| Phocidés. | 30. *Phoca barbata* Fabricius. No. 1926-83. |
| Otariidés. | 31. *Otaria Hookeri* Gray. No. 1874-517. |
| | 32. *Otaria* sp.? No. 1916-80 (avec les parties molles). |
| Trichechidés. | 33. *Trichechus rosmarus* L. (jeune). No. 1926-84. |

A ces spécimens doivent s'ajouter les nombreux Chats et Chiens domestiques examinés par G. M. Iliesco dans ses recherches précédentes, et dont les descriptions ont été utilisées pour la rédaction du présent mémoire. Celui-ci a surtout été établi d'après les pièces squelettiques, les sujets revêtus de leurs parties molles ayant été seulement employés pour le contrôle et un complément d'information.

La bibliographie détaillée de ce travail d'ensemble est la même que celle qui a été déjà donnée dans les mémoires particuliers ci-dessus cités de G. M. Iliesco sur les fosses nasales du Chat et du Chien.

## 1. La Constitution des Parois et la Forme d'ensemble des Cavités Nasales.

Les éléments suivants prennent part à la constitution des parois des cavités nasales chez les Carnassiers :—

En haut : le nasal et le frontal en avant ; l'ethmoïde et une petite partie du sphénoïde en arrière.

En dehors : l'apophyse nasale de l'intermaxillaire et le maxillaire supérieur en avant ; le lacrymal, le palatin (par sa portion verticale) et le ptérygoïde en arrière.

En dedans : la lame perpendiculaire de l'ethmoïde, le cartilage de la cloison qui lui fait suite et le vomer.

En bas : l'intermaxillaire, le maxillaire supérieur et le palatin (par sa portion horizontale).

*Viverridés* *.—Chez les Viverridés, les cavités nasales sont allongées, suivant en cela la forme de la tête.

*Félidés.*—Chez les grands Félidés les cavités nasales sont, comme l'est la tête, très développées en hauteur. Chez le Chat où la face est très courte la cavité nasale est très courte aussi.

Chez la Panthère, le Guépard et le Tigre, son diamètre vertical est à peu près égal à son diamètre longitudinal, ce qui donne à la face un profil bombé, surtout prononcé chez le Guépard et plus encore chez le Tigre.

Il convient de noter que, chez les Félidés, les cavités nasales sont à peu près complètement obstruées dans leurs trois quarts postérieurs par les cornets, qui ne laissent libre à la respiration que le méat inférieur, d'ailleurs remarquable par sa hauteur.

*Hyænidés* †.—Ici, les cavités nasales présentent des caractères

* Les ouvertures des narines sont en forme de virgule à queue très allongée.

† L'appareil cartilagineux du museau est très développé. Ses parties dorsales sont très larges, et le cartilage supplémentaire qui soutient en dehors l'aile de la narine est très grand. Le développement de l'appareil cartilagineux donne au museau une forme tubuleuse et bombée, surtout latéralement ; les orifices des narines sont larges, en forme de virgule, leurs lèvres épaisses et arrondies.

très particuliers, tant au point de vue de la forme que de la capacité. Elles sont allongées et peu hautes; cependant, le cornet maxillo-turbinal étant relativement réduit, le méat inférieur est assez largement ouvert.

*Canidés.*—Voir le mémoire déjà cité de G. M. Iliesco, actuellement en cours d'impression.

*Ursidés.*—Les Ursidés présentent des différences notables au point de vue de la forme de la tête. Celle-ci est très allongée chez l'*Ursus arctos* L., le rapport de la hauteur à la longueur étant de 43 environ; elle l'est moins chez l'*Ursus isabellinus* Horsf. (*syriacus*) (No. 1905-218), où ce rapport n'est que de 34 approximativement.

Les cavités nasales, qui, d'une façon générale, sont très allongées, suivent dans l'ensemble la forme de la tête.

En raison du très grand développement du cornet maxillo-turbinal, dans le sens de la hauteur, le méat inférieur est extrêmement réduit.

*Mustélidés.*—Chez les Mustélidés, les cavités nasales sont très semblables comme forme à celles des Ursidés.

*Procyonidés* *.—Il existe aussi une certaine ressemblance entre les cavités nasales des Procyonidés et celles des Ursidés; mais celle-ci tient surtout à la même augmentation du nombre des cornets ethmo-turbinaux internes, ainsi que nous le verrons plus loin.

*Pinnipèdes* †.—Chez les Pinnipèdes, les cavités nasales ont une forme et une disposition très particulières. La place occupée par les ethmo-turbinaux est très réduite, principalement chez les Phoques et le Morse, tandis que le maxillo-turbinal présente, au contraire, un extraordinaire développement vertical, ce dont il résulte, ainsi que nous le verrons plus loin, que les méats inférieur et moyen doivent être à peu près impénétrables sur le vivant.

L'arrangement des os constituant les parois des cavités est aussi quelque peu différent de ce que nous avons observé chez les Fissipèdes.

Il est à remarquer, par exemple, que, en particulier chez les Phoques, la partie de l'ethmoïde qui intéresse la paroi supérieure, au lieu d'être légèrement inclinée de haut en bas et d'avant en arrière sur l'horizontale, comme elle l'est chez les Fissipèdes, est verticale, dépassant même cette position, puisqu'elle est légèrement inclinée de haut en bas et d'arrière en avant.

Chez le Morse, le vomer est très fort et ne présente, comme chez

* La charpente cartilagineuse nasale des Procyonidés est très étendue, spécialement chez le *Nasua*, où elle dépasse notablement le bord alvéolaire antérieur. Les ouvertures des narines sont très petites et situées à la partie supérieure d'une sorte de pavillon; leur aile externe est très mobile.

† La charpente cartilagineuse du nez de l'Otarie est très réduite; elle est représentée seulement par trois petites pièces plus ou moins cylindriques. La narine a la forme d'une courte fente linéaire, dont l'aile externe n'a aucun support cartilagineux. Les deux orifices sont très près l'un de l'autre, n'étant séparés que par un très petit sillon médian.

l'Otarie d'ailleurs, qu'une partie verticale qui se soude de très bonne heure à l'extrémité antérieure du prosphénoïde.

## 2. Les Cornets.

On distingue chez les Carnassiers comme partout :—

1°. Une série d'ethmo-turbinaux internes dont le premier est désigné sous le nom de naso-turbinal. Ils sont d'habitude plus nombreux que chez les Ongulés. Le premier et les tout derniers mis à part, ils ont aussi pour caractère, examinés sur une coupe parasagittale de la tête, de se recouvrir les uns les autres beaucoup plus largement que chez les Ongulés.

2°. Une, deux ou quelquefois même (Ursidés) trois séries d'ethmo-turbinaux externes.

3°. Un maxillo-turbinal.

Tous ces cornets présentent une beaucoup plus grande ramescence que chez les Ongulés.

### a. *Ethmo-turbinaux.*

*Viverridés.*—Les ethmo-turbinaux internes sont au nombre de 5, decroissant de longueur du 1er au 5ème.

D'après S. Paulli *, la *Genetta genetta* L. a 4 endo-turbinaux, mais la lamelle qui constitue la base du 2ème étant divisée en deux, cela fait bien au total 5 ethmo-turbinaux internes comme nous venons de le dire.

Le naso-turbinal est en rapport dans toute la longueur de son bord inférieur avec le bord supérieur du 2ème ethmo-turbinal interne ; son squelette est formé d'une lamelle osseuse très fine et très friable qui se prolonge jusqu'à la partie antérieure de l'os nasal ; elle a son origine dans la partie interne et moyenne de la lame criblée. De sa région moyenne part un prolongement qui, se fixant sur la face interne du maxillaire superieur, constitue la racine inférieure du cornet, laquelle, sur une coupe parasagittale de la tête, paraît recouverte par le 2ème ethmo-turbinal interne.

La cavite du naso-turbinal est en communication avec le sinus maxillaire.

Ce cornet se prolonge en avant, et il en est ainsi chez tous les Carnivores, par une racine cartilagineuse se terminant en une partie élargie d'un ovale plus ou moins allongé et qui se réunit au cartilage dorsal du museau à plus ou moins de distance de l'ouverture de la narine, mais généralement très près de cet orifice.

Le 2ème ethmo-turbinal interne présente, au milieu de sa face interne, une large dépression où se loge l'extrémité du 3ème. Sur une coupe parasagittale de la tête il paraît recouvrir en avant la moitié supérieure du maxillo-turbinal.

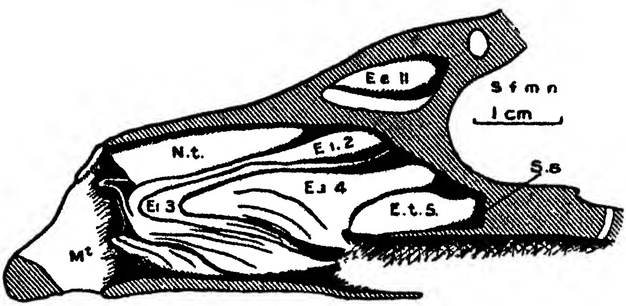
Le 3ème ethmo-turbinal interne se moule dans la dépression de la face interne du 2ème ; la lamelle osseuse qui le constitue se

* S. Paulli. Ueber die Pneumaticität des Schadels bei den Saugethieren. Morphol. Jahrb. Zeitschrift. f. Anat. und Entwickl. 1900.

fixe en bas sur la racine inférieure de ce dernier cornet, qui n'est elle-même qu'une continuation de la lame papyracée. Sa racine ethmoïdale, qui part à peu près exactement au milieu de la lame criblée, est commune avec celle du 2ème ethmo-turbinal interne. Il convient de noter que le 2ème et le 3ème ethmo-turbinaux internes sont des cornets doubles, ayant chacun deux lamelles squelettiques.

Le 4ème ethmo-turbinal interne, logé dans une dépression de la face interne du 3ème, part de la limite supérieure du quart inférieur de la lame criblée un peu en dehors de la ligne médiane. Sa racine osseuse inférieure se comporte comme celle du 3ème. L'insertion commune des racines inférieures des ethmo-turbinaux internes 2, 3, 4 sur la lame papyracée limite en haut l'orifice par lequel le sinus maxillaire s'ouvre dans le méat moyen.

Texte-figure 1.




Coupe parasagittale de la tête osseuse du *Paradoxurus* (No. 1909-35) ; disposition des fosses nasales, côté droit.

Le 5ème ethmo-turbinal interne est le plus petit de toute la série. Il a son origine dans la partie la plus inférieure de la lame criblée. Par son extrémité postérieure il occupe l'entrée du sinus sphénoïdal.

Il est de règle que les ethmo-turbinaux externes de la 1ère série soient au nombre de 9. En dehors, leurs lamelles squelettiques qui d'habitude ne sont que légèrement enroulées se fixent sur la face interne de la portion orbitaire du frontal ; seule, la lamelle du dernier est fixée sur la face interne de la portion verticale du palatin.

Les ethmo-turbinaux externes de la 2ème série occupent des positions très diverses, suivant les types. Ainsi, chez le *Paradoxurus* et chez la *Viverra indica* Desm., où ils sont au nombre de 3 ou de 4, ils remplissent entièrement la cavité du sinus frontal. Chez la Civette, au contraire, où ils ne sont d'habitude qu'au nombre de 2, ils sont seulement fixés par leur extrémité postérieure au pourtour de l'ouverture du sinus frontal, leurs lamelles

osseuses circonscrivant deux orifices incomplets et séparés, par lesquels ce sinus est en communication avec la cavité nasale.

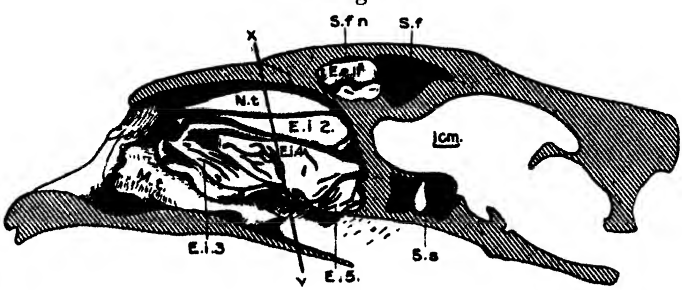
S. Paulli n'a trouvé chez la *Genetta genetta* L. que 5 ecto-turbinaux. Probablement a-t-il considéré comme un seul cornet l'ensemble de tous les cornets qui ont une racine commune.

*Félidés.*—Le Chat a déjà été étudié par l'un de nous *. D'une façon générale, au point de vue de la disposition des cornets, il se rapproche des Viverridés. Ses ethmo-turbinaux internes sont au nombre de 5.

Les ethmo-turbinaux externes de la première série sont au nombre de 7 et ceux de la 2ème au nombre de 5, occupant une position intrasinusienne.

Chez les grands Félidés, les cornets sont dans l'ensemble plus pneumatisés que chez le Chat.

Texte figure 2.




Coupe parasagittale de la tête osseuse du *Felis leo* L. (No. 1918–35); disposition des fosses nasales, côté droit.

Chez le Lion, les ethmo-turbinaux internes sont aussi au nombre de 5.

Le premier ou naso-turbinal prend son origine à la partie supérieure de la lame criblée, en commun avec le 1er ethmo-turbinal externe de la deuxième série. Inférieurement, il se fixe à la face interne du maxillaire supérieur et de la portion orbitaire du frontal. Sa cavité, creusée dans sa partie postérieure, est divisée par des cloisons irrégulièrement disposées. Le compartiment antérieur de cette cavité est en communication avec la cavité nasale par une fente linéaire où s'engage le bord supérieur du 2ème ethmo-turbinal interne. Les compartiments moyen et postérieur débouchent inférieurement par deux fentes relativement étroites.

Le 2ème ethmo-turbinal interne recouvre à peu près toute la moitié supérieure du maxillo-turbinal. Sa racine d'origine est commune avec celle du 3ème ethmo-turbinal interne; sa racine inférieure se fixe à la face interne de la portion orbitaire du

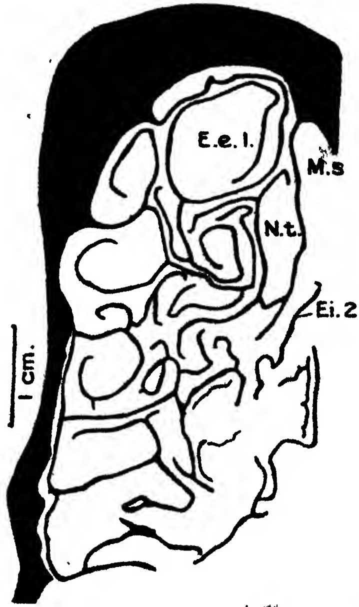
* G. M. Iliesco. *Loc. cit.*

frontal, immédiatement au dessus de la ligne de suture de cet os avec la portion verticale du palatin.

Le 3ème ethmo-turbinal interne, logé dans une dépression de la face interne du deuxième, a sa racine ethmoïdale commune, comme nous l'avons dit, avec celle du 2ème ; sa racine inférieure se fixe également à la face interne de la portion orbitaire du frontal.

Le 4ème ethmo-turbinal interne, logé dans une dépression de la face interne du 3ème, a sa racine ethmoïdale fixée à peu près dans

Texte-figure 3.




Coupe transversale de la demi-tête osseuse droite du *Felis leo* L. (No. 1918–35), pratiquée suivant la ligne XY (voir texte-fig. 2). Procédé de R. Anthony, Bulletin du Mus. d'Hist. naturelle, 1915–1916.

la partie centrale du contour interne de la lame criblée ; elle est, en outre, commune avec celle des 9ème et 10ème ethmo-turbinaux externes de la première série. Sa racine inférieure s'unit à celles des 2ème et 3ème ethmo-turbinaux internes.

Le 5ème ethmo-turbinal interne est relativement développé, et son expansion peut être attribuée au grand développement du sinus sphénoïdal, où il s'engage par son extrémité postérieure. Sa racine ethmoïdale se fixe sur la partie inférieure du contour de la lame criblée et est commune avec les racines des 11ème et 12ème ethmo-turbinaux externes de la première série.

Un fait qui caractérise tous les ethmo-turbinaux internes du

Lion est leur grande pneumaticité, les vastes cavités qui les creusent étant divisées par des cloisons en de très nombreuses logettes. Les ethmo-turbinaux externes de la 1ère série sont au nombre de 12 et, comme nous l'avons noté plus haut, plusieurs d'entre eux ont une origine commune avec les ethmo-turbinaux internes.

Les ethmo-turbinaux externes de la 2ème série sont au nombre de 4, et, en général, plus développés que ceux de la 1ère. Le premier a sa racine ethmoïdale commune avec celle du naso-turbinal, le 3ème avec celle du 1er externe de la 1ère série.

Chez la Panthère, le Guépard et le Tigre, les ethmo-turbinaux sont très semblables à ceux du Lion. Notons cependant que le naso-turbinal paraît présenter chez le Tigre un développement particulier, et que, chez le Guépard, ainsi que chez le Tigre, les ethmo-turbinaux externes des deux séries semblent plus développés que chez le Lion.

*Hyænidés.* - Contrairement à ce que dit Paulli, les ethmo-turbinaux sont, chez les Hyænidés, relativement développés.

Paulli a trouvé chez l'*Hyæna striata* L. 4 endo-turbinaux, mais, la lamelle de base du 3ème étant double, on pourrait dire qu'il existe 5 ethmo-turbinaux internes dans cette espèce, les quatre derniers offrant une grande ressemblance avec ceux de la Civette.

Sur l'exemplaire représenté (texte-fig. 4) il en existe 6.

Le squelette du naso-turbinal affecte une forme à peu près rectangulaire. Par son bord inférieur, ce cornet est, chez l'*Hyæna striata* L. (No. 1899-337) *, en rapport, en avant et en arrière seulement, avec le bord supérieur du 2ème ethmo-turbinal interne; dans sa région moyenne, il est au contact du bord supérieur du 3ème; le 2ème ethmo-turbinal interne est donc à ce niveau complètement caché par une sorte d'expansion du 3ème. Le naso-turbinal prend naissance sur la partie supérieure de la face antérieure de la lame criblée.

La racine postérieure du 2ème ethmo-turbinal interne, commune avec celle du 3ème, est fixée juste au milieu de la lame criblée dans sa partie la plus proéminente. Sa racine inférieure, commune au 3ème et au 4ème, est placée un peu au dessus de la ligne suivant laquelle se soude le maxillaire supérieur avec la portion verticale du palatin, en arrière du lacrymal. L'insertion de cette racine se fait sur un relief déterminant une sorte de crête qui circonscrit partiellement l'orifice du sinus maxillaire.

Ce cornet est constitué d'une lamelle se divisant en deux branches qui s'enroulent en sens contraire. La branche supérieure, qui est la plus développée, décrit une grande spire. La branche inférieure forme une spire incomplète beaucoup plus petite.

Les cavités de l'ethmo-turbinal interne No. 2 sont en communication avec la cavité nasale par les espaces qui restent ouverts entre les spires.

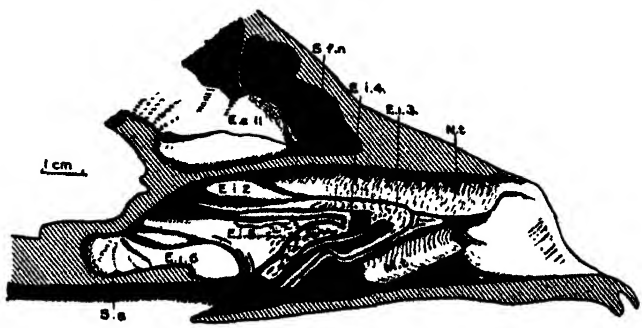
* De grandes différences peuvent exister à cet égard entre les individus.

Le 3ème ethmo-turbinal interne est logé dans une dépression de la face interne du 2ème. De même, le 4ème est logé dans une dépression de la face interne du 3ème.

Le 5ème ethmo-turbinal interne est également logé dans une dépression de la face interne du 4ème ; sa lame d'origine qui décrit une grande spire d'un tour et demi part à peu près du milieu de la lame criblée, ayant une origine commune avec celle du 2ème ethmo-turbinal externe de la 2ème série ; les lames de ces deux cornets se réunissent périphériquement pour s'attacher à la face interne de la portion orbitaire du frontal. Inférieurement, ce cornet se fixe avec les précédents à la face interne de la lame papyracée.

Le 6ème ethmo-turbinal interne est le plus court de tous, mais il est néanmoins bien développé, possédant même une vaste cavité. Il prend naissance dans la partie la plus inférieure de la lame

Texte-figure 4.



Coupe parasagittale de la tête osseuse de l'*Hyæna striata* L. (No. 1899-337 disposition des fosses nasales, côté gauche.

criblée. Sa lamelle constitutive est très fine et elle se dédouble immédiatement après son départ de la lame criblée, les deux feuillets qui résultent de ce dédoublement étant enroulées en sens inverse. Ce cornet obstrue à peu près complètement la cavité du sinus sphénoidal. Sa cavité propre communique avec la cavité nasale par l'espace qui reste ouvert entre ses spires.

Les ethmo-turbinaux externes sont peu nombreux, mais assez bien développés.

Paulli en a trouvé 5 chez l'*Hyæna striata* L., tandis que nous en avons compté 7. Ceux de la 1ère série sont au nombre de 4.

Le 1er est indépendant, et compris entre le 1er et le 2ème ethmo-turbinaux internes ; il a son origine dans la moitié supérieure de la lame criblée.

Le 2ème est plus petit et son origine est commune avec celle de l'ethmo-turbinal interne No. 4.

Le 3ème et le 4ème ont deux racines distinctes, mais leurs

lamelles squelettiques se fixent ensemble à la face interne de la portion verticale du palatin dans sa partie supérieure. Le 3ème est situé en dehors du 5ème ethmo-turbinal interne, le 4ème en dehors de l'espace qui sépare le 5ème et le 6ème ethmo-turbinaux internes.

Les ethmo-turbinaux externes de la 2ème série sont au nombre de 3. Ils sont tous situés à l'intérieur du sinus fronto-naso-maxillaire. Ils sont très développés et très pneumatisés. La racine du 1er s'insère au niveau de la partie interne du contour supérieur de la lame criblée ; en dehors, sa lame s'attache aussi à la face interne de la portion orbitaire du frontal.

Le 2ème est situé au dessus de l'extrémité postérieure du naso-turbinal. Sa racine ethmoïdale est réunie à celle du 1er.

Le 3ème prend son origine tout en haut de la lame criblée ; en dehors, il s'attache à la face interne de la portion orbitaire du frontal.

*Canidés.*—L'étude des cornets ethmo-turbinaux des Canidés ayant fait l'objet d'un travail spécial qui paraîtra prochainement, nous ne ferons ici que rappeler leur nombre.

Les ethmo-turbinaux internes sont au nombre de 5 ; les ethmo-turbinaux externes de la 1ère série au nombre de 10, ceux de la 2ème de 5.

*Ursidés.*--A l'encontre de ce que nous avons observé chez les Carnassiers précédents, les ethmo-turbinaux internes sont ici situés tous, sauf le premier ou naso-turbinal, en arrière bien plutôt qu'au dessus du maxillo-turbinal.

On compte 7 à 8 ethmo-turbinaux internes. Chez l'*Ursus arctos* L. (No. 1918-40) nous en avons trouvé 7, mais chez l'Ours orné (No.1848-369) nous en avons pu compter 8. Nous en avons également observé 8, du côté droit, chez l'*Ursus maritimus* Desm. du Spitzberg (No. 1869-71).

S. Paulli compte chez l'*Ursus arctos* L. 4 endo-turbinaux avec 7 cornets, parce que les lamelles basales du 3ème et du 4ème se divisent respectivement en 2 et 3 feuillets.

Le naso-turbinal est très allongé, ressemblant à celui du Chien. Dans sa partie moyenne, il présente un gonflement remarquable répondant à sa cavité divisée en un grand nombre de logettes et qui descend jusqu'au milieu de la cavité nasale. Son squelette est représenté par une lame osseuse qui, chez l'*Ursus isabellinus* Horsf. (*syriacus*), devient très forte avec l'âge. Il prend naissance à la partie supérieure de la lame criblée. Inférieurement, il se fixe à la lame papyracée.

L'ensemble des autres ethmo-turbinaux internes (2-3-4-5-6 et 7) forme une masse d'un volume relativement réduit. La longueur de chacun d'eux diminue régulièrement du 1er au dernier. Tous sont caractérisés par le fait que leur surface est lisse au lieu de présenter les nombreux plissements que l'on observe chez les autres Carnassiers. Leurs cavités sont divisées en logettes, et tous prennent leur origine à la partie interne et

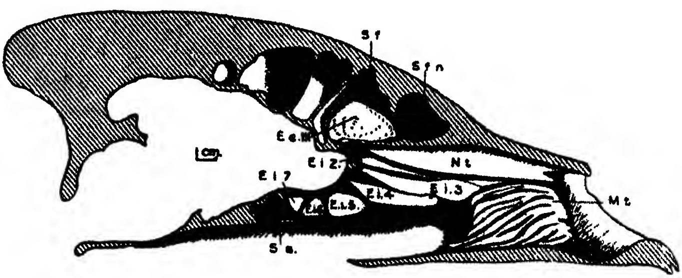
inférieure de la lame criblée. Inférieurement, tous sont, en outre, fixés à la lame papyracés.

En arrière de la masse constituée par les derniers ethmo-turbinaux internes est une lamelle osseuse qui, dépendant de l'ethmoïde et faisant immédiatement suite à la lame criblée, sépare le sinus sphénoïdal en deux compartiments. Le compartiment postérieur est une cavité libre, tandis que l'antérieur est entièrement occupé par les trois derniers ethmo-turbinaux internes.

Le 2ème ethmo-turbinal interne a sa racine ethmoïdale réunie à celle du 3ème.

L'ensemble des ethmo-turbinaux externes constitue une masse extrêmement complexe. Tous sont très divisés, mais leur division est irrégulière. Ils ont toujours des racines communes avec les ethmo-turbinaux internes. Ils sont très nombreux et leur nombre, ainsi que leur situation, est variable suivant les

Texte-figure 5.




Coupe parasagittale de la tête osseuse de l'*Ursus arctos* L. (No. 1918–40) ; disposition des fosses nasales, côté gauche.

espèces. Ainsi, chez l'*Ursus arctos* L. (No. 1918–40), très différent des autres formes à cet égard, ils sont beaucoup plus nombreux qu'ailleurs et leur disposition est aussi différente.

Disposés chez l'*Ursus isabellinus* Horsf. (No. 1905–218) en deux séries, comme chez tous les autres carnivores, ils forment trois séries chez l'*Ursus arctos* L., une première située en dehors des 1er, 2ème, 3ème, 4ème, 5ème et 6ème ethmo-turbinaux internes, une deuxième située au dessus de la précédente dans le fond de la cavité nasale, et enfin une troisième constituée d'éléments très développés, très pneumatisés et qui s'implantent par leurs racines au plafond de la lame criblée. Cette troisième série est entièrement logée à la partie inférieure du premier compartiment du sinus frontal, les éléments les plus postérieurs étant situés au dessus de la partie antérieure de l'hémisphère cérébral.

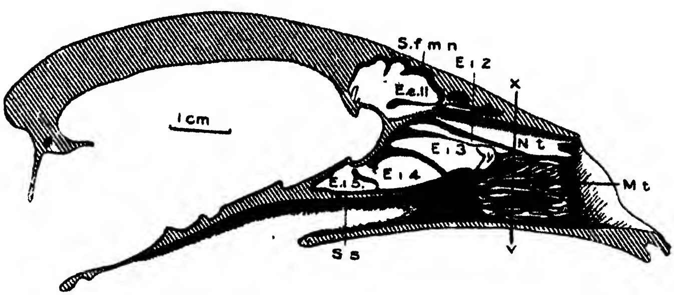
S. Paulli a trouvé chez l'*Ursus arctos* L. 9 ethmo-turbinaux externes. Nous pouvons affirmer qu'ils sont beaucoup plus nombreux.

Les racines des ethmo-turbinaux externes paraissent disposées en séries linéaires, mais sinueuses, à la surface de la lame criblée. Cette disposition s'observe très bien chez l'*Ursus isabellinus* Horsf., où l'on voit 8 lignes de racines disposées à peu près parallèlement.

On peut estimer que les Ours possèdent plus de 40 ethmo-turbinaux externes; les plus nombreux sont toujours ceux de la troisième série lorsque cette série est distincte. Ceux qui sont les plus externes sont fixés en dehors à la portion orbitaire du frontal. Parmi ceux de la troisième série, il en est quelques-uns qui se fixent aussi à la cloison qui sépare le compartiment le plus antérieur du sinus frontal de la cavité nasale.

*Mustélidés.*—Chez les Mustélidés, la forme et la disposition des cornets est très voisine de celles qui s'observent chez les Ursidés. Mais, le nombre des ethmo-turbinaux internes est seulement de 5, ceux-ci ayant d'ailleurs la même origine que chez les Ours.

Texte-figure 6.




Coupe parasagittale de la tête osseuse du *Meles taxus* Bodd. (No. 1901-626); disposition des fosses nasales, côté gauche.

D'après S. Paulli, le *Meles taxus* Bodd. possède 4 endo-turbinaux avec 7 lamelles enroulées.

Il faut aussi remarquer que les ethmo-turbinaux internes sont ici plus développés que chez les Ursidés relativement au volume de la tête.

Le naso-turbinal est assez développé. Sa cavité n'est pas subdivisée en logettes; sa racine inferieure est située au dessus de la racine de la dernière molaire.

Les ethmo-turbinaux externes s'attachent tous en avant par l'intermédiaire de la lame papyracée, soit à la face interne du maxillaire supérieur, soit à celle de la portion verticale du palatin. Leur ensemble constitue une masse volumineuse qui s'étend jusqu'à la face supérieure de la portion horizontale du vomer à laquelle elle adhère.

Les ethmo-turbinaux externes de la 1ère série sont au nombre de 14 chez le Blaireau d'Europe (No. 1900-386). Plusieurs d'entre eux sont fixés à la lame criblée sur une même lame osseuse

qui est commune quelquefois aussi aux cornets internes. Les deux cornets externes les plus inférieurs de cette 1ère série s'attachent en bas à la face supérieure de la portion horizontale du vomer.

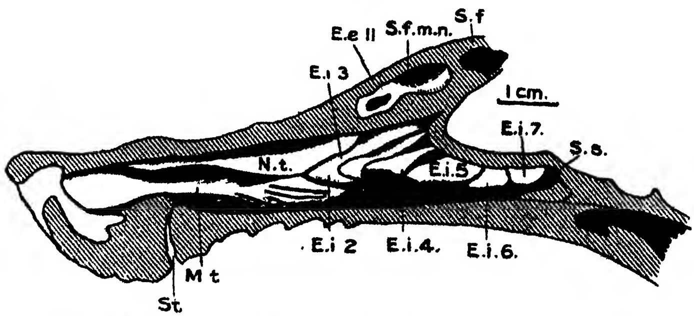
Les ethmo-turbinaux externes de la 2ème série sont au nombre de 12 chez le Blaireau d'Europe; ils sont logés dans la cavité du grand sinus fronto-maxillo-nasal.

S. Paulli a trouvé chez cet animal 10 endo-turbinaux, mais il a certainement compté les cornets multiples pour un seul et c'est vraisemblablement de là que provient son erreur.

Inférieurement, les ethmo-turbinaux externes de la 2ème série sont fixés soit à la face interne du frontal, soit à la face interne de sa portion orbitaire, soit à la face externe de sa lame sagittale.

*Procyonidés.*—Chez les Procyonidés, le nombre des ethmo-turbinaux internes est à peu près le même que chez les Ursidés. La disposition d'ensemble est aussi celle des Ursidés.

Texte-figure 7.




Coupe parasagittale de la tête avec les parties molles du *Nasua narica* L. (No. 1923-2400) ; disposition des fosses nasales, côté gauche.

D'une façon générale, ces cornets sont également plus allongés que chez les Mustélidés, mais ils ont un volume plus réduit, présentant au point de vue de la forme une certaine ressemblance avec ceux du Chat.

Les 2ème, 3ème, 4ème, 5ème, 6ème, 7ème et 8ème se fixent par leurs racines osseuses inférieures à la partie horizontale du vomer.

S. Paulli a trouvé chez le *Procyon cancrivorus* G. Cuv. 6 endo-turbinaux, le 2ème étant double, ce qui fait en totalité 7 ethmo-turbinaux internes. Nous n'avons pas examiné cette espèce, mais le *Procyon lotor* L. en possède 7. Nous en avons aussi trouvé 7 chez le *Nasua narica* L. (*fusca*).

Le 7ème ethmo-turbinal interne est engagé dans la cavité du sinus sphénoïdal par son extrémité postérieure.

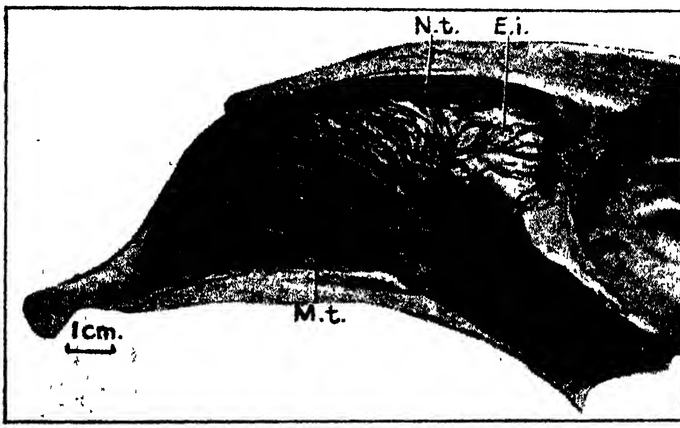
Les ethmo-turbinaux externes de la 1ère série sont au nombre de 10; le 1er, le 2ème et le 3ème d'une part, le 4ème et le 5ème d'autre part, le 9ème et le 10ème enfin ont leurs racines d'origine

communes sur la lame criblée. Ces cornets sont aussi fixés périphériquement à la face interne du maxillaire supérieur, quelques-uns d'entre eux s'attachant au bord postérieur de la lame papyracée.

Les ethmo-turbinaux externes de la 2ème série sont au nombre de 4; ils remplissent la cavité du sinus fronto-maxillo-nasal et sont également fixés périphériquement à la face interne de l'os frontal et aussi sur une petite étendue de la partie supérieure des faces internes des os nasal et maxillaire supérieur.

*Pinnipèdes.*—Chez les Pinnipèdes, les ethmo-turbinaux sont toujours beaucoup moins développés que chez les Fissipèdes. Chez le Morse, leur squelette est très fortement ossifié, même chez le jeune.

Texte-figure 8.




Coupe parasagittale de la tête osseuse du *Phoca barbata* Fabr. (No. 1926–83); dispositions des fosses nasales, côté droit.

Les ethmo-turbinaux internes sont au nombre de 7 chez le Phoque, de 9 chez l'Otarie, de 6 seulement chez le Morse.

S. Paulli a trouvé 5 endo-turbinaux chez le Phoque avec 6 cornets, le deuxième étant formé de deux lamelles enroulées ayant la même origine.

Ce groupe des ethmo-turbinaux internes, à l'exception du premier qui s'étend jusqu'aux narines, constitue chez tous les Pinnipèdes une masse peu volumineuse occupant le fond de la cavité nasale, de forme plus ou moins carrée chez le Phoque et le Morse, rectangulaire, c'est-à-dire plus développé dans le sens longitudinal, chez l'Otarie. L'extrémité antérieure de cette masse s'engrène plus ou moins, ainsi que celle de la masse constituée par les ethmo-turbinaux externes, avec les ramifications

postérieures du maxillo-turbinal ; ceci est surtout net chez le Morse et l'Otarie.

Les espaces qui séparent les ethmo-turbinaux internes sont toujours très réduits.

En raison de la brièveté de l'os nasal chez l'Otarie, la surface d'insertion de la lame d'origine du naso-turbinal sur la crête turbinale de cet os est extrêmement réduite. De plus, ce cornet ne possède pas de racine inférieure.

Parmi les autres ethmo-turbinaux internes, il en est quelques-uns qui ont leur racine d'origine commune avec celle du cornet voisin, comme, par exemple, cela s'observe chez l'Otarie pour les cornets 2 et 3, ainsi que pour les cornets 4 et 5, ou avec celle d'un ethmo-turbinal externe.

Les ethmo-turbinaux externes sont disposés en une seule série, ce qui est en rapport avec l'absence de tout sinus chez les Pinnipèdes, ainsi que nous le verrons plus loin.

Ils sont peu nombreux, leur nombre variant suivant les espèces. Nous avons pu en compter 8 chez le Phoque, d'un volume relativement réduit et d'une forme peu compliquée. S. Paulli a également trouvé 8 ecto-turbinaux chez l'*Halichœrus gryphus* Fabr.

En résumé, les ethmo-turbinaux sont beaucoup moins nombreux et beaucoup moins développés chez les Pinnipèdes que chez les Fissipèdes. Les externes sont groupés en une seule série.

### β. *Maxillo-turbinal.*

Ce cornet présente chez les divers carnivores de très grandes différences de forme et de complication ; celle-ci atteint son maximum chez les Mustélidés et les Ursidés, mais surtout chez les Pinnipèdes.

*Viverridés.*—Chez les Viverridés, le maxillo-turbinal a une forme allongée ; il occupe presque toute la moitié inférieure de la fosse nasale.

Sa lame d'origine sur le maxillaire supérieur se prolonge antérieurement au delà de l'apophyse nasale de l'intermaxillaire et se termine en arrière sur un relief situé au dessus de la racine de la deuxième molaire chez la Civette, au dessus de celle de la 1ère chez le Paradoxure (No. 1909–35).

Cette lame d'origine ne porte qu'une seule volute qui est inférieure, et qui décrit une spire d'un tour et demi à peu près. En bas, elle se prolonge par une petite lamelle secondaire incomplètement divisée par 2 ou 3 sillons. De même, sur la face supérieure de la lame d'origine, on peut observer quelques lamelles secondaires peu développées, disposées dans le sens de la longueur.

En résumé, le maxillo-turbinal des Viverridés est volumineux, développé dans le sens longitudinal ; mais il ne présente qu'une seule volute qui est inférieure et simple.

*Félidés.*—Chez le Chat domestique le maxillo-turbinal est simple de forme et sa division dichotomique est incomplète et irrégulière.

Chez le Lion, au contraire, il est remarquable par son grand développement ; son squelette commence en avant un peu en arrière de la suture intermaxillo-maxillaire, s'étendant jusqu'à l'union du tiers antérieur et du tiers moyen de la portion verticale du palatin.

Sa lame d'origine porte deux volutes enroulées en sens inverse, l'une supérieure, l'autre inférieure, celle-ci plus développée (un tour et demi de spire) et se divisant en deux branches qui se réunissent en arrière à la lame primaire d'où elles partent.

Chez le Tigre, le Guépard et la Panthère, le maxillo-turbinal a la même forme que chez le Lion, mais il paraît être relativement moins volumineux.

*Hyænidés.*—Chez les Hyænidés, le maxillo-turbinal est d'un volume relativement réduit et d'une forme assez simple, ce qui fait que le méat inférieur est très large dans toute sa longueur.

Sa lame d'origine porte deux ailes, enroulées en sens inverse, la supérieure l'étant moins que l'inférieure.

*Canidés.* – Le maxillo-turbinal du Chien est très développé, présentant une ramification dichotomique importante et à peu près régulière.

*Ursidés.* --Chez les Ursidés, le maxillo-turbinal est court, mais extraordinairement développé dans le sens de la hauteur et très ramifié ; la racine postérieure de sa lame d'origine est située au niveau de la partie antérieure de la dernière molaire chez l'*Ursus arctos* L. (No. 1918–40) et au niveau de l'espace qui sépare la dernière molaire de l'avant dernière chez l'*Ursus isabellinus* Horsf. : elle est fixée au maxillaire supérieur sur un relief osseux très prononcé. Ce cornet occupe toute la hauteur de la partie moyenne de la cavité nasale, s'étendant du plafond jusqu'au plancher. En raison de ce développement extraordinaire, les deux méats, moyen et inférieur, sont très réduits.

Sa lame d'origine porte deux ailes, l'une supérieure, l'autre inférieure, enroulées en sens inverse. Sur leur face interne, et, chez l'*Ursus isabellinus* Horsf. (No. 1905–218), même sur leur face externe, ces ailes primaires donnent naissance à des ailes secondaires qui sont variables en nombre suivant les espèces.

Chez l'*Ursus isabellinus* Horsf. (No. 1905–218) et chez l'*Ursus arctos* L. de l'Ile Sakhaline (No. 1900–76) les ailes secondaires provenant de l'aile primaire supérieure sont au nombre de 3, tandis que, chez l'*Ursus arctos* L. (No. 1918–40), elles sont au nombre de 5. Chacune d'elles se divise à son tour après un court trajet en deux ailes tertiaires, celles-ci en deux ailes quaternaires et celles-ci même en deux ailes du 5ème ordre. Les dernières ailes finissent par se réunir à nouveau suivant le même système pour s'insérer à la racine osseuse postérieure.

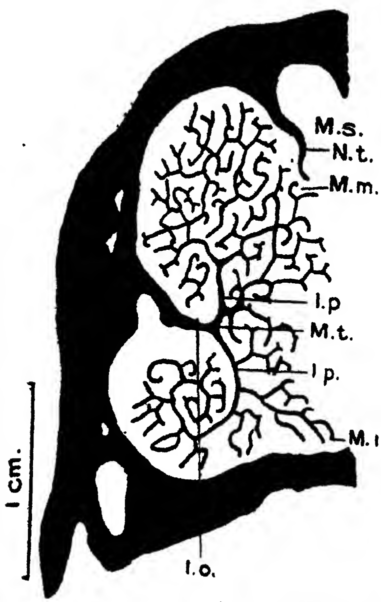
L'aile primaire inférieure donne naissance d'habitude à 5 lamelles secondaires, dont il est de règle que la 4ème soit très développée et très ramifiée. Chez l'*Ursus isabellinus* Horsf (No. 1905–218) nous en avons trouvé 6. Toutes se divisent de la

même manière que celles de l'aile primaire supérieure et finissent aussi à la racine postérieure.

Les ailes secondaires sont très courtes et non enroulées, tandis que les tertiaires, quaternaires et du 5ème ordre sont plus longues, plus enroulées, mais toujours irrégulièrement.

En résumé, les caractères du maxillo-turbinal chez les Ursidés sont les suivants: son grand développement dans le sens de la hauteur et sa ramescence extrêmement riche.

Texte-figure 9.




Coupe transversale de la demi-tête osseuse droite du *Meles taxus* Bodd. (No. 1901-626) pratiquée au milieu de la longueur du maxillo-turbinal suivant la ligne XY (voir texte-fig. 6), pour montrer la grande ramescence de ce cornet. Procédé de R. Anthony, Bulletin du Mus. d'Hist. naturelle, 1915-1916.

*Mustélidés.*—Chez les Mustélidés, le maxillo-turbinal se rapproche, comme forme et mode de division, de celui des Ursidés ; il est beaucoup plus divisé que chez les Chiens. Court et très développé dans le sens de la hauteur, il obstrue à peu près complètement la lumière de la cavité nasale. Sa lame d'origine porte deux ailes très enroulées, et qui donnent naissance à des lames secondaires.

Chez le Blaireau d'Europe, l'aile primaire supérieure porte 8 ames secondaires et l'inférieure 6, chaque lame secondaire portant à son tour deux ailes tertiaires, et celles-ci, pour la plupart, deux ailes quaternaires.

A peu près au milieu de la longueur du cornet, ces lames s'associent à nouveau et toujours deux par deux pour finir ensemble à l'extrémité postérieure.

En résumé, les caractères fondamentaux du maxillo-turbinal chez les Mustélidés sont, comme chez les Ursidés, son grand développement dans le sens vertical et sa très grande ramescence.

*Procyonidés.*—Chez les Procyonidés, le maxillo-turbinal ressemble beaucoup à celui des Canidés, avec cette différence que, chez le *Procyon* par exemple, il est plus divisé.

De son grand développement résulte que le méat inférieur est très réduit. La racine osseuse postérieure est placée, chez le *Procyon*, au dessus de l'alvéole de la première molaire.

La lame d'origine porte deux ailes plus enroulées que chez le Chien et qui se subdivisent jusqu'au 5ème ordre. L'aile primaire inférieure est la plus importante et forme avec ses branches à peu près les trois quarts du volume entier du maxillo-turbinal ; elle porte 6 lamelles secondaires qui, à leur tour, se ramifient, toujours suivant le système dichotomique. L'aile primaire supérieure est moins divisée et ne porte que 2 ailes secondaires, qui sont aussi moins divisées que celles de l'aile inférieure.

*Pinnipèdes.*—Chez les Pinnipèdes, le maxillo-turbinal atteint un plus grand développement et une plus grande complication que partout ailleurs. Son grand développement paraît s'établir au dépens des ethmo-turbinaux qui sont très réduits, surtout chez le Phoque et chez le Morse. Il est si développé dans le sens de la hauteur que, chez l'animal vivant, la muqueuse doit obstruer plus ou moins complètement la cavité nasale dans sa partie moyenne. Les méats moyen et inférieur étant ainsi à peu près supprimés, seul le méat supérieur reste bien discernable.

La racine de ce cornet est à peu près horizontale chez le Phoque et chez l'Otarie, plus large et plus inclinée de haut en bas et de dehors en dedans chez le Morse. Elle s'étend en avant chez le Morse et chez l'Otarie jusqu'à l'apophyse nasale de l'intermaxillaire, se terminant chez le Phoque et le Morse un peu en arrière de la dernière molaire et chez l'Otarie au niveau de l'avant-dernière. Le mode de subdivision de la lame d'origine est différent de celui que nous avons constaté chez les Fissipèdes, bien que les dispositions observées chez les Ursidés, les Mustélidés et les Procyonidés y conduisent.

Chez le Phoque, il y a deux lames primaires, qui ne sont que peu enroulées, la supérieure présentant 4 divisions secondaires et l'inférieure 5 ; celles-ci à leur tour portent d'autres branches de plus en plus divisées. Nous avons pu suivre cette division dichotomique jusqu'à des branches du 8ème ordre.

Chez l'Otarie, de la face supérieure de la lame d'origine, on voit partir 7 branches primaires, les deux premières ayant une racine commune ; de sa face inférieure, presque accolées à la paroi inféro-latérale de la cavité nasale, partent 3 branches primaires seulement ; elles se subdivisent jusqu'au 4ème ordre.

C'est chez le Morse que le maxillo-turbinal atteint le plus grand

développement. Les branches primaires de la face supéro-interne de sa lame d'origine sont au nombre de 6. Elles peuvent se subdiviser jusqu'au 6ème ordre, et, comme chez tous les Pinnipèdes, ces branches de subdivision sont d'autant plus flexueuse qu'elles appartiennent à un ordre plus élevé. Toutes se regroupent à nouveau en arrière, d'où il résulte que la plus grande ramescence du cornet s'observe à sa partie moyenne.

En résumé, les caractères fondamentaux du maxillo-turbinal chez les Pinnipèdes sont : un développement tel dans le sens de la hauteur qu'il doit obstruer la cavité nasale, et sa très grande ramescence.

### 3. Les Méats.

Chez les Carnassiers, comme partout, le méat supérieur ne contient aucun orifice. Le méat moyen présente toujours l'orifice du sinus maxillaire, le méat inférieur celui du canal de Stenson toujours perméable et celui du conduit lacrymal dans sa partie antérieure.

*Viverridés* et *Félidés.*—Le méat supérieur est proportionnellement plus large chez les Viverridés et chez les grands Félidés que chez le Chat.

*Hyænidés.*—Le méat supérieur est représenté par une gouttière particulièrement large et profonde. L'orifice du canal de Stenson dans le méat inférieur est au niveau de l'alvéole de la canine, celui du canal lacrymal à un niveau un peu plus antérieur.

*Canidés.*—Chez les Canidés, le méat supérieur est semblable à celui des Viverridés et des grands Félidés.

*Ursidés.*—Chez les Ursidés, le méat inférieur, qui est d'abord très large, devient extrêmement réduit au niveau du maxillo-turbinal en raison du grand développement de ce cornet dans le sens de la hauteur. Il redevient très large en arrière.

Par le fait d'une particularité remarquable, les Ursidés possèdent à la marge de l'orbite deux trous lacrymaux, l'un antéro-supérieur, l'autre postéro-inférieur percé à l'union du lacrymal et du maxillaire supérieur. L'orifice lacrymal dont on note la présence à l'avant du méat inférieur correspond seulement au premier de ces trous ; au second correspond un canal qui débouche à la paroi externe du sinus maxillaire sur une petite éminence.

*Mustélidés.*—Chez les Mustélidés le méat supérieur ressemble beaucoup à celui de l'Hyène. Par contre, le méat moyen ressemble plutôt à celui du Chien.

Le méat inférieur est assez large sauf dans sa partie moyenne où il devient très étroit par suite du grand développement du maxillo-turbinal dans le sens de la hauteur.

*Procyonidés.*—Chez les Procyonidés, le méat supérieur est assez large et bien délimité comme chez le Chien.

Le maxillo-turbinal chez le *Procyon* étant très développé et remplissant à peu près complètement la partie antérieure de la cavité nasale, l'espace que représente le méat moyen est si réduit

qu'il n'existe guère en réalité au niveau de ce cornet. Il en est à peu près de même du méat inférieur.

Le canal de Stenson s'ouvre un peu en arrière des incisives.

*Pinnipèdes.*—Chez les Pinnipèdes, le méat supérieur est une étroite et profonde gouttière.

Les méats moyen et inférieur sont, en raison de l'extrême développement du maxillo turbinal, à peu près supprimés. Il semble que chez l'animal vivant la communication des voies respiratoires avec l'extérieur ne puisse se faire que par la bouche.

Chez tous les Pinnipèdes, le canal lacrymal fait défaut.

## 4. Les Sinus.

*Viverridés.*—Chez les Viverridés, on compte 3 ou 4 sinus.

Chez la *Viverra indica* Desm., ainsi que chez le *Paradoxurus*, il en existe 3 : un sinus fronto-maxillo-nasal, un sinus maxillaire et un sinus sphénoïdal.

Chez la Civette, il en existe 4 : un sinus frontal, un sinus fronto-maxillo-nasal, un sinus maxillaire et un sinus sphénoïdal.

Le sinus frontal est simple et creusé entièrement dans l'os frontal. Il est situe en arrière de son apophyse orbitaire et, par sa moitié postérieure, il surplombe le lobe olfactif et même la partie antérieure de l'hémisphère cérébral.

Le sinus fronto-maxillo nasal est une très large cavité s'étendant aux deux portions du frontal (frontale proprement dite et orbitaire), au maxillaire supérieur, à la partie postérieure de l'os nasal et à la lame sagittale de l'ethmoïde. Cette grande cavité est entièrement occupée par les cornets ethmo-turbinaux externes de la 2ème série et en large communication avec la cavité nasale par l'intermédiaire des espaces qui séparent ces cornets. Elle est aussi en communication directe avec le sinus frontal, par la cavité d'un cornet externe de la 2ème série et avec le sinus maxillaire.

Le sinus maxillaire est une cavité bien circonscrite qui intéresse non seulement le maxillaire supérieur, mais aussi le lacrymal. Sa limite antérieure est au niveau du trou sous-orbitaire.

Le sinus sphénoïdal creusé dans le prosphénoïde présente, chez les Viverridés, des différences notables de capacité. Celle-ci est très réduite chez le *Paradoxurus*, tandis que chez la Civette ainsi que chez la *Viverra indica* Desm., elle est relativement vaste. Elle est toujours et à peu près complètement occupée par l'extrémité postérieure du dernier ethmo-turbinal interne.

*Félidés.*—Il existe chez le Chat trois sinus : frontal, fronto-nasal et sphénoïdal, ce dernier étant très développé. Le sinus maxillaire fait défaut.

Chez les grands Félins, on compte de chaque coté 4 sinus : un sinus frontal, un sinus fronto-nasal, un sinus sphénoïdal et un sinus maxillaire.

Le sinus frontal s'étend aussi à la partie antérieure du pariétal. Il est divisé en logettes, dont le nombre est variable, par des

cloisons assez fortes, mais incomplètes. Sa cavité est en communication avec celle du sinus fronto-nasal par un large orifice obturé à peu près complètement par l'extrémité postérieure d'un ethmo-turbinal externe de la 2ème série par la cavité duquel s'établit en réalité cette communication.

Chez le Tigre, le sinus frontal est plus réduit, et sa cavité n'est pas divisée en logettes. Il est en communication directe avec la cavité du sinus fronto-nasal par un large orifice qui est occupé en partie par l'extrémité postérieure de deux ethmo-turbinaux externes de la 2ème série; mais il présente une particularité digne d'être remarquée en ce que les extrémités de ces deux cornets sont complètement occluses.

Le sinus frontal chez la Panthère est très spacieux et divisé en plusieurs logettes, surtout en arrière et en dehors.

Chez le Guépard, ce sinus est encore plus vaste, et est aussi divisé en logettes, mais mieux individualisés que chez la Panthère.

Chez ces deux dernières espèces, Panthère et Guépard, le sinus frontal n'est pas en communication directe avec le sinus fronto-nasal, mais l'est par l'intermédiaire d'un ethmo-turbinal externe.

Le sinus fronto-nasal chez le Lion est à peu près de la même grandeur que le sinus frontal; sa cavité est toujours entièrement occupée par les ethmo-turbinaux externes de la 2ème série qui sont très développés. Il communique avec la cavité nasale par l'intermédiaire de ces cornets.

Le sinus fronto-nasal chez le Tigre est plus développé que le sinus frontal avec lequel il est en communication directe, comme nous l'avons déjà dit. Sa cavité est, ainsi que chez le Lion, occupée par les ethmo-turbinaux externes de la 2ème série.

Il en est de même chez la Panthère et le Guépard.

Le sinus sphénoïdal chez le Lion est très développé; son orifice de communication avec la cavité nasale est plus qu'aux deux tiers occupé par le 5ème ethmo-turbinal interne.

Ce sinus est aussi assez spacieux chez la Panthère et chez le Guépard, étant même relativement plus développé que chez le Tigre. Sa cavité est occupée par l'extrémité postérieure du 5ème ethmo-turbinal interne chez le Tigre et la Panthère; mais chez le Guépard ce cornet s'arrête à l'entrée de la cavité du sinus sphénoïdal.

Le sinus maxillaire chez le Lion est d'une capacité relativement réduite.

Il est encore plus réduit chez le Tigre et le Guépard, et surtout chez la Panthère.

La réduction du sinus maxillaire, qui est même inexistant chez le Chat, est donc un caractère général des Félins.

*Hyænidés.*—Chez les Hyænidés, les sinus frontal et fronto-nasal sont extrêmement développés. Dans l'intérieur du sinus frontal existe un grand cornet largement enroulé et par l'intermédiaire duquel ce sinus communique avec la cavité nasale. Le sinus fronto-nasal, dont l'intérieur est incomplètement divisé en

deux grands compartiments par une cloison osseuse très épaisse, présente dans la partie postéro-interne de son compartiment postérieur deux grand cornets ethmo-turbinaux externes de la 2ème série, par l'intermédiaire desquels sa cavité communique aussi avec la cavité nasale.

Le sinus sphénoïdal est vaste. Sa cavité est complètement remplie par le 6ème ethmo-turbinal interne très développé. Le sinus maxillaire existe.

*Canidés.*—On compte chez le Chien quatre sinus: frontal, fronto-nasal, ethmoïdal et maxillaire *.

*Ursidés.*—Chez les Ursidés on compte 4 sinus : frontal, fronto-nasal, sphénoïdal et maxillaire.

Le sinus frontal est une cavité d'habitude très spacieuse et qui atteint son plus grand développement chez l'*Ursus arctos* L. dans sa partie cranienne, tandis que chez l'*Ursus isabellinus* Horsf. et chez l'Ours blanc c'est plutot dans sa partie faciale qu'il s'étend. Il présente des dimensions variables suivant les types. Ainsi, il est moins développé chez l'*Ursus isabellinus* Horsf.; il l'est peu aussi chez l'Ours blanc. Chez l'*Ursus arctos* L. (voir texte-figure 5) sa cavité est divisée en 4 compartiments. Chacun de ces compartiments, sauf le dernier, communique séparément avec la cavité nasale par un orifice situé toujours à sa pointe inférieure.

S. Paulli a trouvé aussi chez l'*Ursus arctos* L. 4 compartiments dans le sinus frontal.

La cavité du premier compartiment est occupée par les ethmo-turbinaux externes de la 3ème série qui ont leurs racines implantées au plafond de la lame criblée.

Chez l'*Ursus isabellinus* Horsf., ainsi que chez l'Ours blanc (No. 1869–71), le sinus frontal n'est divisé qu'en deux compartiments, dont l'antérieur est le plus grand et en même temps occupé à peu près entièrement par les ethmo-turbinaux externes de la 2ème serie qui sont très développés. Ces deux compartiments communiquent séparément avec la cavité nasale.

Le sinus fronto-nasal est une grande cavité simple qui, chez l'*Ursus arctos* L., a une forme allongée. Il se prolonge en avant par une grande excavation creusée dans la partie postérieure de l'os nasal. Ce sinus présente sur son plancher une très large ouverture par laquelle il communique avec le sinus maxillaire. Il ne communique pas avec le sinus frontal.

Le sinus sphénoïdal est très grand chez l'*Ursus arctos* L. (No. 1918–40) et moins développé chez l'*Ursus isabellinus* Horsf. et chez l'Ours blanc. Il occupe toute la longueur du prosphénoïde, s'étendant même, chez l'*Ursus arctos* L., à la partie antérieure du sphénoïde postérieur. Ce sinus, qui présente en avant une logette latérale assez importante, est divisé en deux compartiments par une lame qui dépend du prosphénoïde : le compartiment postérieur communique directement avec la cavité nasale ; le compartiment

* Voir pour plus de détails, G. M. Iliesco, mémoire à paraître prochainement.

antérieur est occupé entièrement par les 3 derniers ethmo-turbinaux internes.

Le sinus maxillaire est représenté chez les Ours par une cavité bien délimitée, à la paroi externe de laquelle est percée l'ouverture du conduit lacrymal postéro-inférieur.

*Mustélidés.*—Chez les Mustélidés, il existe trois sinus : un grand sinus fronto-maxillo-nasal, un sinus sphénoïdal et un sinus maxillaire.

Le sinus fronto-maxillo-nasal est très développé par rapport à la grandeur de la tête et à la taille des animaux. Sa cavité est creusée dans la plus grande partie de l'os frontal et est entièrement occupée par les ethmo-turbinaux externes de la 2ème série, par l'intermédiaire desquels elle communique avec la cavité nasale.

Le sinus sphénoïdal est relativement bien développé, toujours creusé dans le corps du prosphénoïde et occupé par les deux derniers ethmo-turbinaux internes.

Le sinus maxillaire s'ouvre dans le méat moyen par un orifice situé en arrière de la racine postérieure du maxillo-turbinal.

*Procyonidés.*—Chez les Procyonidés, il existe 4 sinus : un sinus frontal, un sinus fronto-maxillo-nasal, un sinus sphénoïdal et un sinus maxillaire.

Le sinus frontal, chez le *Procyon*, est représenté par une cavité assez grande et simple, creusée entièrement dans l'os frontal. Cette cavité est en communication avec la cavité nasale par l'intermédiaire du 4ème cornet ethmo-turbinal externe de la 2ème série, dont l'extrémité postérieure s'insère au pourtour d'un orifice par lequel ce sinus s'ouvre en avant dans le sinus fronto-maxillo-nasal.

Le sinus fronto-maxillo-nasal est un peu plus vaste que le sinus frontal. Sa cavité, qui communique avec celle du sinus frontal, est entièrement occupée par les ethmo-turbinaux externes de la 2ème série ; inférieurement, il est limité par la lamelle du naso-turbinal et par la lame papyracée. Il est en communication avec la cavité nasale par les espaces qui séparent les ethmo-turbinaux externes de la 2ème série.

La cavité du sinus sphénoïdal creusée dans le quart antérieur du prosphénoïde est occupée par les deux derniers ethmo-turbinaux internes.

Le sinus maxillaire n'est représenté chez le *Procyon* que par une cavité relativement réduite située immédiatement en arrière de l'extrémité postérieure du maxillo-turbinal.

*Pinnipèdes.*—Chez les diverses espèces de Pinnipèdes, tous les sinus font défaut. On peut observer, en arrière du maxillo-turbinal et au dessous des ethmo-turbinaux, une vaste dépression limitée en dehors par la portion orbitaire du frontal et par la portion verticale du palatin, en bas par la portion horizontale de ce dernier os. Cette dépression, qui se trouve en large communication avec l'arrière fond des fosses nasales, ne représente pas un véritable sinus.

## Résumé.

Les variations de forme des cavités nasales chez les Carnassiers suivent dans l'ensemble les variations de forme de la tête : par exemple, les cavités nasales des Viverridés sont étroites et allongées, celles des Félidés courtes et hautes.

Il existe aussi, suivant les types, des variations quant à la disposition des os qui prennent part à la constitution des parois des cavités nasales. A cet égard, l'ensemble des Pinnipèdes se montre différent de l'ensemble des Fissipèdes.

Les Carnassiers sont remarquables par le grand nombre de cornets qu'ils peuvent quelquefois posséder, par la grande ramescence de ceux-ci et par un recouvrement beaucoup plus large que chez les Ongulés, par exemple, des ethmo-turbinaux internes de la région moyenne, les uns par rapport aux autres.

Le tableau ci-dessous indique le nombre des ethmo-turbinaux généralement existant dans chaque famille :—

| | Fissipèdes. | | | | | | | Pinnipèdes. | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | *Æluroidea.* | | | *Cynoidea.* | *Arctoidea.* | | | *Arctoidea.* | | |
| | Viverridés. | Félidés. | Hyænidés. | Canidés. | Ursidés. | Mustélidés. | Procyonidés. | Otariidés. | Phocidés. | Trichechidés. |
| Ethmo-turbinaux internes | 5 | 5 | 6 | 5 | 7-8 | [illegible] | 7 | 9 | 7 | 6 |
| Ethmo-turbinaux externes | | | | | | | | | | |
| „ „ 1ère série .. | 9 | 12 | 4 | 10 | 40 environ. | 14 | 10 | [illegible] | 8 | ? |
| „ „ 2ème série | 3-4 | 4 | 3 | 5 | | 12 | 4 | 0 | 0 | 0 |
| „ „ 3ème série . | 0 | 0 | 0 | 0 | | 0 | 0 | 0 | 0 | 0 |

Au point de vue de la forme, de la disposition et du nombre de leurs cornets, les Carnassiers se divisent naturellement en deux grands groupes.

Les Viverridés, Félidés, Hyænidés sont caractérisés par un faible nombre d'ethmo-turbinaux, un maxillo-turbinal peu élevé, mais développé dans le sens antéro-postérieur, relativement simple de constitution.

Les Ursidés, Mustélidés, Procyonidés sont caractérisés : 1°, par un nombre d'ethmo-turbinaux sensiblement plus grand—ceux-ci atteignent leur maximum de nombre chez les Ursidés où les ethmo-turbinaux externes peuvent même comprendre 3 séries, ce fait paraissant être en rapport avec le grand développement de

leurs organes olfactifs ; 2°, par la complication de ces ethmo-turbinaux ; 3°, par un maxillo-turbinal court, mais très développé de haut en bas, d'une constitution extrêmement complexe.

On remarquera que ces deux groupes correspondent exactement aux Ailuroïdes d'une part et aux Arctoïdes de l'autre, sous ordres établis d'après un ensemble de caractères auxquels il faut maintenant ajouter ceux des cavités nasales.

Les Canidés (Cynoïdes) sont à cet égard, comme à tous les autres, intermédiaires entre les Æluroïdes et les Arctoïdes. On notera qu'au point de vue des cavités nasales, ils se rapprochent surtout des premiers.

Les Pinnipèdes sont par le nombre, la disposition et la forme de leurs cornets, comme à tous les autres points de vue, de véritables Arctoïdes. Leur maxillo-turbinal est semblable à un maxillo-turbinal d'Ursidé ou de Mustélidé, atteignant même un plus grand volume et une beaucoup plus grande complication. La régression de leurs ethmo-turbinaux tant en grandeur qu'en nombre est en rapport tout à la fois avec le grand développement de leur maxillo-turbinal et avec le peu d'importance de leurs fonctions olfactives.

Le méat inférieur est partout d'autant moins large que le maxillo-turbinal est plus élevé : en effet, il est relativement spacieux chez les Æluroïdes, beaucoup moins chez les Arctoïdes Fissipèdes, pratiquement supprimé chez les Pinnipèdes dont le méat moyen est aussi à peu près inexistant. Chez ces derniers animaux, il semble que le passage de l'air aux voies respiratoires ne puisse guère se faire que par la bouche.

Le conduit de Stenson, qui, comme l'on sait, s'ouvre dans le méat inférieur, est toujours perméable chez les Carnassiers.

Au point de vue du canal lacrymal, qui s'ouvre constamment dans le méat inférieur, il convient d'insister sur la particularité présentée par les Ursidés. Ces animaux ont deux trous lacrymaux, à chacun desquels correspond un canal lacrymal ; de ces deux canaux lacrymaux, l'un s'ouvre dans le méat inférieur, l'autre dans le sinus maxillaire.

Les sinus sont au nombre de 3 ou 4 suivant les types : frontal, fronto-nasal et, quelquefois, chez certains types, fronto-maxillo-nasal, sphénoïdal, maxillaire. Par le fait d'une exception unique, ce dernier sinus n'existe pas chez le Chat ; chez les grands Félins, et aussi chez les Procyonidés, il est de taille relativement réduite.

Dans la cavité du sinus frontal (chez les Hyænidés), fronto-nasal ou fronto-maxillo-nasal, sont logés les ethmo-turbinaux externes de la 2ème série, ou même ceux de la 3ème série chez les Ours, qui seuls possèdent ces cornets.

Chez les Pinnipèdes, il n'existe aucun sinus cranio-facial.

## *Signification des Lettres employées dans les Texte-figures.*

***N.t.***—Naso-turbinal.

***E.i.***—Ensemble des Ethmo-turbinaux internes.

***E.i.* 2**, ***E.i.* 3**, ***E.i.* 4**, ***E.i.* 5**, ***E.i.* 6**, ***E.i.* 7** — Ethmo-turbinaux internes.

***E.e.* I.**—Ensemble des ethmo-turbinaux externes de la 1ère série.

***E.e.* II.**—Ensemble des ethmo-turbinaux externes de la 2ème série.

***E.e.* III.**—Ensemble des ethmo-turbinaux externes de la 3ème série.

***M.t.***—Maxillo-turbinal.

***l.o.***—lame d'origine.

***l.p*** —lame primaire.

***M.s.***—Méat supérieur

***M.m.***—Méat moyen

***M.i.***—Méat inférieur

***S.f.***—Sinus frontal.

***S.f.n.***—Sinus fronto-nasal.

***S.f.m.n.*** - Sinus fronto-maxillo-nasal

***S.s.***—Sinus sphénoïdal.

***St.***—Canal de Stenson.

# 51. On the Crop Contents of certain Mallophaga.

By Dr. James Waterston, F.Z.S.

(Offered for publication by permission of the Trustees of the British Museum.)

[Received May 25, 1926: Read October 19, 1926.]

(Text-figure 1.)

In the Mallophaga, as is well known, the crop is a conspicuous feature of the anterior portion of the alimentary tract. Frequently it can be seen without dissection, and it has been figured now for a considerable number of species. Three main forms of the organ are known. In the Liotheidæ the crop is a more or less distinct and simple enlargement of the posterior œsophagus, separated from the ventriculus by a constriction. In the Ischnocera generally, it is a pear or tadpole shaped sac, broadest anteriorly (where it opens both to the œsophagus and to the ventriculus, the openings being at about the same level) and tailing off considerably posteriorly; while in the Trichodectidæ it is a separate sac-like structure connected with the œsophagus by a narrow tube. The following notes are concerned only with crops of the first two types. As seen through the integument the crop (generally blackish in colour) lies obliquely across the abdomen with the broad end on the right anteriorly, while the narrow apical portion reaches far back on the left. During life it undergoes periodic compression and contraction (?), appearing to flatten out from time to time posteriorly and to shift slightly forward, after which it recovers its original position and shape. In *Goniodes bicuspidatus* (on *Tragopan* spp.) the rate of this pulsation is much slower than that of the dorsal vessel. As the "tail" flattens out one can see the long feather fibres within and the agitation of smaller particles. In the crop of this type the chitinous intima is longitudinally striate or finely plicate, the striæ being well marked posteriorly—*i. e.*, towards the "tail." On the broad anterior end, slightly in advance of the inlet and outlet of the organ, is an area set with teeth variable in shape and disposition. Commonly they range from 1·2 $\mu$ in length. They may occur singly or in short comb-like rows, each with a continuous chitinous base, and together forming a more or less dense apical cap, easily appreciated when the crop has been slit open and its contents evacuated. One special arrangement (found in certain Sand-Grouse parasites) may be referred to where the combs of teeth are parallel and succeed one another at intervals, forming a longitudinal row for some distance down the side of the crop.

Nothing seems to come amiss to the Mallophaga as food.

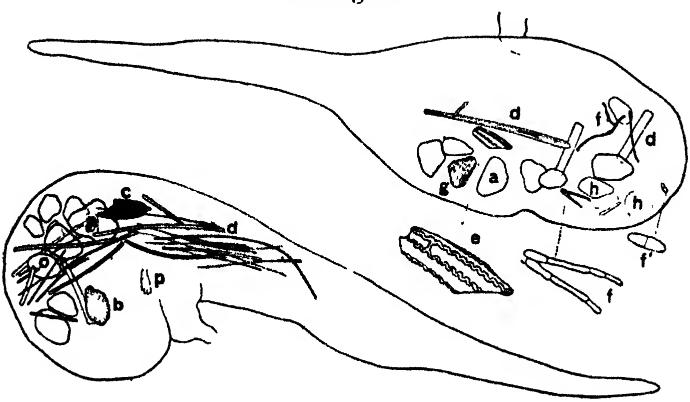
The protecting sheaths of growing feathers, feather fibre, down, skin, scurf, scabs, blood (when available), etc., are all eaten; they devour, too, their own egg-shells and cast-off skins and perhaps occasionally indulge in cannibalism, for I have recently examined a crop of the large *G. bicuspidatus* which was crammed solely with fragments of *Goniocotes diplogonus*, some of which appeared not to be of exuvial origin.

If the crop of a Philopterid is examined after its owner has fed some time on one of the stiffer feathers of its host, it will often be found to be packed with sections of barb of a length equal to the crop itself. Sometimes, however, the fibre is in shorter lengths. The further breaking up of the food appears to be affected by the movements of the organ already noted, whereby the crop-contents are squeezed forward and rubbed against the rasp-like teeth, the tiny fragments thereafter flowing for digestion into the ventriculus, whose contents are always homogeneous, and where I have never seen unaltered fibre. If this view of the function of the crop-teeth is correct, the crop, it is obvious, is at the same time to some extent a gizzard. Where the combs of teeth are set in a longitudinal row, they also probably help to guide the fibre to the apex of the crop. The chitinous and other comestibles in a Philopterid crop, however, are far from exhausting its contents. For four years I have been taking intermittent notes on this subject, and perhaps I can best indicate the unexpected variety of these inclusions by describing a concrete example. Owing to its resistance to clearing agents the crop of the Mallophaga is apt to be a source of trouble in the preparation of mounts. Hence, it has been my custom for some time past to remove the crop, and either discard or mount it separately. While examining the freshly removed crop of *Esthiopterum monile* Gieb. ♀ taken on a tawny vulture (*Neophron pileatus*), Africa, Kenya Colony, Ithanga Hills, 20.vii.1921 (H. Wilkinson Coll.), I noted a number of small refringent granules, sufficiently hard to bend the tip of a fine steel needle. These granules did not break or crumble when mounted under pressure (upper figure), and when examined by polarised light were seen to consist of three different minerals, the bulk being quartz.

As no special care had been exercised in extracting the crop to avoid breakage (by which extraneous bodies might have gained entrance into the organ), a second example of the *Esthiopterum* was selected and the crop dissected out intact and undistorted in any way. This second specimen chanced to be less congested with food than the first, but contained about the same number of granules lying aggregated together at the broad end immediately behind the patch of teeth. In the process of mounting, a slight separation of the granules was caused by the cover-slip (see lower figure). In a number of preparations of lice from other hosts and regions, it seems

that this anterior position is that normally occupied by the granules, and, though no observations on the point have been possible, it is difficult to resist the conclusion that when present they act as accessory triturating agents like the stones in the crop of a bird.

Text-figure 1.




The following is a complete list of the foreign bodies and their dimensions found in the two crops under discussion. Here I should like to thank heartily my colleagues Mr. W. Campbell Smith, Dept. of Geology, and Mr. J. Ramsbottom, Dept. of Botany, for the time and care they have ungrudgingly spent with me in the study of these preparations to ensure accurate determination. The measurements are given in terms of $\mu$ ( = ·001 mm.).

*Contents of Crops of* Esthiopterum monile *Gb.*

Length of crop about 1·8 mm. Breadth over ·4 mm.

*a.* (and all unlettered grains). Quartz. Large pentagonal grain (above *h*) l. = 96 $\mu$, b. = 72 $\mu$, other grains 50–65 $\mu$ by 40–45 $\mu$.

*b.* Mica. l. = 90 $\mu$, b. = 52 $\mu$.

*c.* Lepidopterous scale. l. = 130 $\mu$.

*d.* Feather fibre.

*e.* Portion of seed-coat (cereal ?). l. = 90 $\mu$.

*f.* Conidial form of a Pyrenomycete *Cladosporium* sp. (probably *C. herbarum* (Pers.) Link.). Cells, l. = 20–30 $\mu$, b. = 4–5 $\mu$.

*f*[1]. Spore (probably of *f*). Total length 13 $\mu$ (segments 7 and 6), breadth 3 $\mu$.

*g.* Olivine or pyroxene. l. = 64 $\mu$, b. = 60 $\mu$.

*h.* Felspar (outline indefinite).

*o.* Globule of organic detritus.

*p.* Cuticular process ? of insect larva.

Crop-teeth up to 2 $\mu$; ribands up to 20 $\mu$ with 1, 3, 7, 9 teeth.

Two comments on the above inclusions may be offered :—

*General nature.* The minerals are all derivable from rocks of an igneous region, and the quartz, felspar, and mica might have come from any sand in a granitic area. The other elements are more fortuitously associated, but it is worth noting that I have seen the same or a very similar mycelium and conidiophore in the crop of a *Lagopœcus* from Spitzbergen.

*Origin.* While it is obvious that the above objects must have been taken in with the food, the conditions of their deposition on the host's feathers are less certain. *Esthiopterum monile* occurs mainly on the (?) secondaries of the wing in a position, one would suppose, of security against such accidental fouling of the vulture's plumage as occurs when the bird is feeding or on the ground. On the other hand, all might have been deposited on the feathers of the stretched-out wing in soaring at no great height. The size of the grains indicates probably a local origin, for the smallest pieces of quartz measured are over twice the maximum recorded for fine long-travelling dusts (see W. Campbell Smith in Bannerman, 'The Canary Islands,' Appendix A, p. 323, London, 1922).

*Other instances.* Since first observing these mineral inclusions I have noted their occurrence in crops of an *Esthiopterum* from Marabout Stork (Africa); Philopterids from Hornbill (E. Asia); *Lagopœcus* etc. from Gallinaceous birds (various localities). Permanent mounts have been made of the preparations above described, and can be seen at S. Kensington by anyone interested in the subject.

In conclusion, I may add a note on the crop of the Liotheidæ. Here a most striking difference is to be seen in the crop "teeth," which are large gently-curved scimitar-like structures with a spreading chitinous base. Applied to such structures the word "teeth" is a misnomer, for no evidence that they function as such has ever been forthcoming, and careful (longitudinal) sectioning of *Colpocephalum patellatum* shows that in their natural position these curved flat blades lie parallel to one another across the crop posteriorly with their apices just resting on a fold of the opposite wall. The lumen of the crop is thus occluded to everything unable to pass between the blades, which in association appear to form, and doubtless function as, a filtering or sifting grid. On the method of its working, however, no details have been yet ascertained.

# 52. The Annual Increment of the Antlers of the Red Deer (*Cervus elaphus*) *. By Julian S. Huxley, M.A., F.Z.S.

[Received June 7, 1926: Read October 19, 1926.]

(Text-figures 1–3.)

Considering the varied biological interest of the subject, singularly few accurate data are available on the growth of deer antlers. It was therefore with great interest that I discovered that Captain C. E. Lucas, of Warnham Court, Sussex, had since the year 1893 collected all the shed antlers of the famous Warnham herd of Red Deer, and had kept continuous series of all the best heads. He kindly put this unique material at my service; and with his help and that of Mr. Frank Wallace, 254 pairs of antlers belonging to 32 deer of this herd were weighed. I should here like to tender my thanks to these two naturalist-sportsmen for their interest and help.

In addition, one series of antlers from the same herd (No. 1 in the Tables) had previously been weighed and recorded by Mr. J. G. Millais (see Wallace, 1914), and another (No. 34) had been sent to Dr. J. Ritchie, of the Royal Scottish National Museum, Edinburgh, who has kindly furnished me with the weights. Further, Capt. Dollman, of the Natural History Museum, has been good enough to weigh for me the series of antlers exhibited there (No. 35 in the Tables); and I have found one or two other records (Nos. 36 and 37) in the paper of Dombrowski (1889).

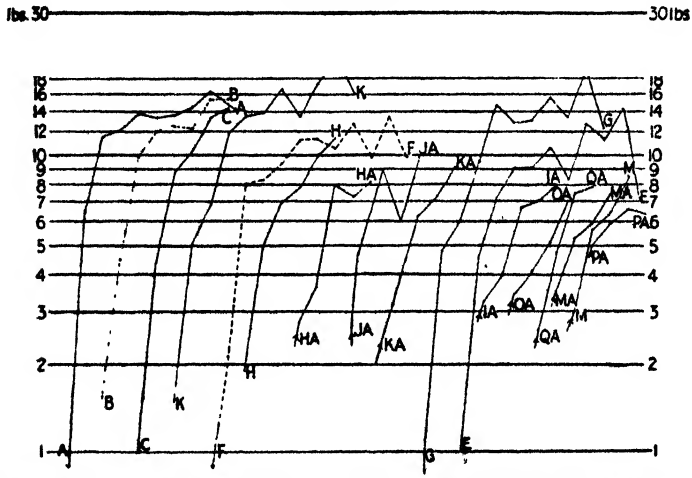
The weighings at Warnham were taken with a previously-tested spring balance. Sometimes points or larger pieces had been broken off the antlers in fighting. These have been roughly allowed for. When animals were killed, the antlers were often mounted on the stuffed head, or on the skull (without lower jaw). In the former case, the weight could not be obtained; in the latter case, allowance has been made for the weight of the skull. This, in one case, in which the antlers were sawn off, was determined and found to be 3¼ lbs. According to skull-length, from 2 to 3½ lbs. have been allowed for skull-weight; weights corrected thus are shown in brackets ( ). Many of the shed antlers had been mounted on light wooden shields. The weight of these was found to vary between 15 and 17 oz.: 1 lb. has accordingly been allowed for them throughout. Series mounted on shields, whose weights have therefore been thus corrected, are marked with an S. No allowance has been made for change of weight with lapse of years, since so little is known on the subject.

* Studies in Heterogonic Growth, No. 2.

The results have been tabulated in various ways.

(1) Each individual antler-weight is recorded in Table I., according to the serial number of years of antler-growth: "1st year" antlers means that pair of antlers whose shedding occurred when the beast was about 1¾ years old; and whose

Text-figure 1.




The growth-curves of antler-weight in 17 individual Warnham Court stags. The weights in lbs. of the successive pairs of antlers are plotted logarithmically, the time is plotted arithmetically (each point indicating a year). The spacing of the various curves is merely for convenience; they are not arranged in any temporal or other sequence. The slope of the curve from point to point is thus directly proportional to the growth-rate (positive or negative) for that year. Arrows at the base of the curves indicate that the weight of the 1st pair of antlers is not plotted. In some cases this weight was not recorded: when the arrow crosses the base line, the weight was recorded but was under 1 lb.

Note the individual differences between stags—*e.g.* between G and E; PA and QA; F and K. Note the considerable fluctuations from the expected curve, which should bend over gradually, then become horizontal, and then descend. These fluctuations are noticeable both during the early years of rapid growth (HA, JA, 5th antlers; M and MA, 4th antlers; IA, K, 3rd antlers), where they appear as irregularities in the ascent of the curve; and in more mature stags, in which actual regression followed by later increase may occur (E, F, G, K, etc.). Some beasts show much less variation of this type than do others (*e.g.* A, B). The final regression before death may be very heavy (*e.g.* G and especially E).

growth began at about 8–10 months and continued till 13–15 months. The percentage increment (or decrement) for the antler-weight of the current year over that of the previous year is also recorded. A graphic record of the annual growth

for a number of individual stags is given in text-fig. 1. The weights have here been plotted logarithmically, since when this is done, the slope of the curve is directly proportional to the rate of growth, which can then be seen at a glance.

The percentage increments can also be plotted against age (not here figured). It is then seen that there is a steady decline up to 5 or 6 years (after which time much irregularity obtains: this is doubtless mainly due to seasonal conditions or to disease—see later).

No stag, of those with 10 or more years of antler-growth, attained its maximum antler-growth later than its 13th antler-pair or earlier than its 9th; the mean was 10·56, but the mode (6 out of 11) was 10th. All but 1 of the 11 specimens showed decrease of antler-weight in years later than that of the maximum. This one exception (V) was accidentally killed.

In addition, two specimens (B and M) which only grew 9 pairs of antlers, showed a decline after reaching a maximum with their 7th and 8th pair respectively.

The earliest years of antler-growth in which any stag's antlers decline is the 3rd, in which LA shows a very slight decrease of 2 ozs. (0·7 per cent.). None of the 4th sets of antlers show a decrease, though F and O show increases of only 3·1 and 2·3 respectively. In the 5th year of antler-growth, 5 out of 34 specimens show decreases, up to 32·9 per cent. In the 6th year, 10 out of 29 do so; in the 7th, 5 out of 20; in the 8th, 7 out of 17; in the 9th, 4 out of 14; in the 10th, 3 out of 12: in the 11th, 5 out of 9; in the 12th, 4 out of 5; in the 13th, 1 out of 3; and in the 14th, 2 out of 2.

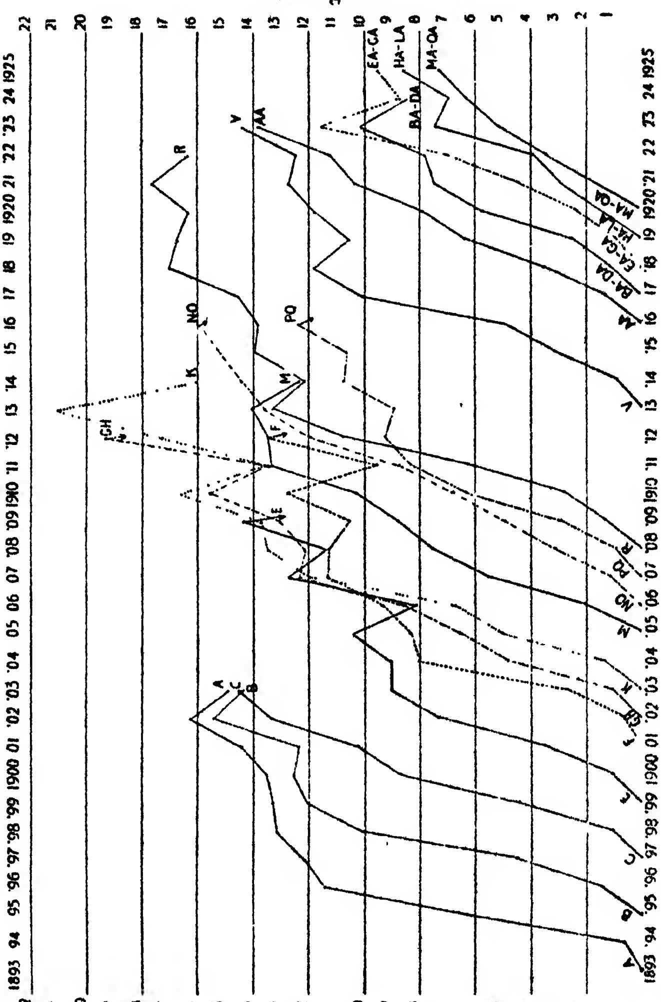
The percentage of those showing decreases thus increases very regularly, as follows:—

| 2nd | 3rd | 4th | 5th | 6th + 7th | 8th + 9th | 10th + 11th | 12th + 13th + 14th | year of antler-growth. |
|---|---|---|---|---|---|---|---|---|
| 0 | 2·9 | 0 | 14·7 | 29·8 | 34·9 | 40·3 | 71·0 | % of antlers showing [decreases from previous year. |

It is very remarkable that No. 15 (R), who died of old age, showed so little regression in the last year of his life.

At the bottom of Table I. are given almost the only facts I can find recorded as to the growth of stags in total weight—and they are only put forward as estimates. They were made by the late H. Evans for the weight of deer on his forest in Jura (see Evans, quoted by Cameron, 1923). It is clear, I think, that he was here and there in error, notably in regard to the increment from 1st to 2nd years, which certainly cannot be less than the 2nd to 3rd year increment. In my opinion the 1st-year weight is too high, and 60 lbs. would be nearer the mark (for further discussion see a subsequent paper in this series of studies, on the relation between body-weight and antler-weight in Red Deer).

Text-figure 2.



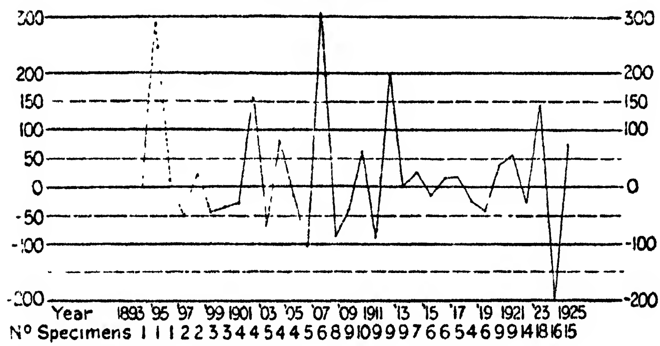
To indicate the effects of season on antler-growth. The individual antler-series of 33 Warnham Court stags (Nos. 1–33, Table I.) have been grouped according to date of birth. When more than one animal has been born in one year, the mean for all born in that year has been taken. Downward-pointing arrows indicate marked "going back" in antler-weight, due to old age or disease, the final weight not being plotted: *e.g.* E, F, and G + H. Sometimes when one of the stags born in the same year has regressed markedly before the other, the final years have not been plotted (*e.g.* N + O after 1916).

Ordinates, weight of antlers in lbs.: abscissæ, dates from 1893 to 1925. Note the coincidence of diminutions or increases in growth-rate (in young animals) or in absolute weight (in mature stags) in particular years: *e.g.*, depressions in 1924, 1922, 1911, 1906; favourable effects in 1923, 1921, 1912, 1910, 1907, 1902.

The means of the weights and the increments for each year-class have next been calculated, and the results are presented in Table II. The first section (A) comprises the means for all of specimens 1–33; the second (B) for all among these specimens whose antler-weights appear in two successive years; and the third (C) for 11 specimens whose antler-weights are known for 10 successive years. (B) is here taken as the best standard.

Next, the material was classified according to date, as opposed to the previous classification by age only. The results are given graphically in text-fig. 2, where the means for all the stags born in any one year are plotted.

Text-figure 3.




To indicate the effect of the year on antler-growth of 33 Warnham stags (Nos. 1–33, Table I.). (1) The percentage increment of each antler-weight over that of the same stag in the previous year was found; (2) the percentage deviation of this increment from the mean increment for all animals of the same age was next calculated; (3) the mean of all the percentage deviations for each particular year was then taken. These means are here plotted for the years from 1894 to 1925. The numbers of individual deviations for each year is given below the year: when there are less than 3 deviations, dotted lines are employed. On this method, 1923, 1912, 1907, and 1902 (and probably 1895—1 specimen) emerge as very favourable years; and 1924, 1911, 1908, 1906 as very unfavourable.

In addition, the increments for each calendar year were examined, and the deviation of each from the mean increment of its age-group was found. This deviation was then calculated as a percentage of the mean increment. By adding together all these percentage deviations, a quantitative expression for the effect of the season on antler-growth can be obtained. If all or most of the deviations are markedly positive, the conditions must have been exceptionally favourable for antler-growth, and *vice versâ*. These results are given in Table III. and plotted graphically in text-fig. 3. Dotted lines are used when only

three animals or less were available for the particular year. Mean percentage deviations of over $-100$ clearly indicate that a decrease instead of an increase in antler-weight occurred for that year.

It will be seen at a glance that some years are highly favourable, others highly unfavourable to antler-growth. I do not pretend that the results have any claim to quantitative accuracy. A single very large deviation not due to season but to sickness or other cause might cancel out a number of small deviations which really represented the climatic effect of the season *. Deviations may perhaps tend to be larger for the very early or very late years than during the middle of growth (though this does not seem to be borne out by the table). I do not therefore attach much weight to mean deviations for the season of under 50 per cent. But in the years 1901 to 1925 there are 6 deviations of from $\pm 50$ to 100 per cent., 3 of $\pm 100$ to 195 per cent., and 3 of over $\pm 195$ per cent. Further, especially in the case of these largest deviations, all or practically all of the individuals deviate in the same direction. In 1924, with a negative mean deviation of $-200$ per cent., only 1 out of 16 specimens had a plus deviation. In 1923, with a positive mean deviation of $+143$ per cent., only 2 out of 18 were negative. In 1912, only 2 out of 12 were of opposite sign to the mean, in 1906 and 1907 one out of 5, in 1902 none out of 4. 1923 and 1924 are years which to me are the most convincing, owing to the large number of specimens. Furthermore, before I started weighing the specimens, Captain Lucas told me that I should find 1923 a good and 1924 a very bad year. He prophecies now (early May, while the antlers are still half-grown) that 1926 will be a very good antler year. The unfavourable influence of 1924 is perhaps best seen by noting the effect on the younger stags. The mean percentage increment for the five stags which had their 4th pair of antlers in 1924 was not much more than half the normal, while the mean of the five which grew their 5th pair in that year showed an actual decrease in absolute antler-weight of about 6 per cent., as against the mean increment for that year of $+18{\cdot}1$ per cent. Absolute decreases were also shown by those which had their 6th and those which had their 7th pair in that year,—decreases of 15·5 per cent. and 23 per cent. respectively. Thus, as would be expected, the bad season does not cause a decrease in absolute antler-weight (as opposed to a negative deviation from the mean increment) while the animal and its antlers are still growing rapidly. An absolute decrease is first seen in the animal's 5th year; in older animals it becomes progressively greater.

Conversely, 1923 produced an absolute weight-increment of nearly 30 per cent. in a 10th year stag, as opposed to the

* NOTE:—*E. g.*, specimen No. 34 became affected with lung-disease in 1921. Note its enormous decline in antler-weight in 1922.

mean increment of about 10 per cent., while in 5th and 6th year stags it increased the weight by nearly 45 per cent., as against the normal increments of 18 per cent. and 13 per cent. respectively.

The favourable and unfavourable years, judging by all methods, appear to be as follows (moderately favourable or unfavourable in brackets):—

favourable... .. 1895 (1 spec. only), 1902, (1904), 1907, 1910, 1912, 1921, 1923, (1925).
unfavourable... (1903), 1906, 1908, 1911, (1919), (1922), 1924.

As to what particular concatenation of circumstances brings about such notable effects on antler-growth,—that question I propose to leave to the meteorologists and physiologists. In general, Captain Lucas believes that favourable circumstances are (1) An early rut, and therefore more time to recover before antler-growth is due to begin. (2) The accumulation of reserves of fat, etc., between the rut and the beginning of antler-growth. Good acorn and beech-mast years favour this, as do also mild winters. (3) Rich feeding during the period of velvet, especially during its earlier part (April and May). At Warnham, the condition of the grass is the determining factor. In 1924 the grass at this time was always soaked with rain and the weather cold. In 1923 there was warm weather, with fine periods alternating with showers.

In a subsequent paper I propose to adduce evidence (based chiefly on the data of Dombrowski, 1889) that, *on the average*, antler-weight in Red Deer is related to body-weight according to the formula $y=bx^k$, which I have already shown (Huxley, 1924) to hold good for the growth of the claws of *Uca*, the Fiddler-crab, where $y$=weight of organ (antlers), $x$=weight of body, and $b$ and $k$ are constants. $k$ appears for antlers to be about 1·5.

The evidence is conclusive that the relative antler-weight steadily rises with absolute body-size, from about 2·5 per cent. in stags of average (clean) body-weight of 80 kg., to about 4·2 per cent. in those of 200 kg. body-weight. These are all from records of *adult* stags, shot by sportsmen; but the evidence further indicates, though as yet (for lack of an equal body of data) not so conclusively, that the same relation, with the same values of $b$ and $k$, holds good for young, rapidly-growing animals as well.

If this is so, we must ask what is implied when the absolute antler-weight *decreases* from one year to the next? This question is especially cogent in the case of young animals, such as that of the stags which were in their 5th, 6th, and 7th years (and therefore would normally be still actively growing) in 1924. Was the absolute decrease in their antler-weight correlated with or produced by an absolute decrease in their body-weight; or can antler-weight be absolutely decreased

while body-weight is only relatively decreased—*i.e.* merely shows less increment than normal? It is at present impossible to answer this question. I can only express the hope that any one who may have the opportunity in zoological garden, park, or laboratory, of weighing deer and their shed antlers year by year, preferably under experimental conditions, will do so. It may be pointed out that since antler-growth is confined to a few months, only the total weight during and immediately preceding those months need be taken into account. Further, if I may express a mere opinion, I incline to the view that an absolute decrease in antler-weight will only occur with an absolute decrease in body-weight, though naturally the latter will be relatively smaller. We know that a stag may lose 5 to 10 per cent., possibly more, of its weight, during the few weeks of the rut: so that even in a growing stag there would be nothing improbable in a loss of 2 or 3 per cent., due to marked poorness of condition, in spite of an absolute increase in, *e.g.*, skeleton-weight.

We already know the normal increments in antler-weight for the Warnham stags. When we know also the normal increments for body-weight; and if further we determine that the same formula holds for the relation between antler- and body-weight throughout life: then we shall be able to calculate with reasonable accuracy, from the data for the stags which were in their 4th, 5th, 6th and 7th years in 1924, what were their actual changes in body-weight in that year.

Certain further facts are worth noting. Up to and including 1904, the park at Warnham was regularly treated with bone-meal or lime, one half of the park being treated one year, the other half the next. Since that time only basic slag has been applied. Bone-meal has again been applied this last year.

It appears quite definite that antler-growth has been less since the lime was discontinued.* The specimens can be arranged by dates of birth into four groups—1893–7, 1897–1903, 1905–1908, and 1916-1920 (inclusive). The solitary specimen born between 1909 and 1915 agrees pretty closely with the last group. When the mean antler-weight and increments for the first 6 years are calculated for each group, and also the maximum weight attained subsequent to 6 years in those which survive this age, the following results are obtained.

The absolute weights for all the years after the 1st thus decline progressively with date. The behaviour of the maxima will not be clear until the more recently-born animals have grown older.

The behaviour of the increments is interesting. There is a decline in the later period of the 2nd and 3rd year increments, but an increase of the 4th and 6th year increments, the 5th year's being

* In addition, it would appear that the earlier series were more specially-selected, the later series, especially Nos. 24–38, giving a more average picture. That this is not the main cause of the falling off, however, is shown by the fact that the best of the later years are far behind the best and the medium of earlier years.

irregular. It would appear that exceptionally rapid growth early, though it will lead to absolutely larger antlers in the 3rd to 6th years, is partly compensated for by a slackening of growth later. Further data, however, would be needed to prove this point satisfactorily.

TABLE A.

| | | 1893–7. | 1897–03. | 1905–08. | 1916–20. |
|---|---|---|---|---|---|
| No. of Specimens .... . | | 3 | 5 | 6 | 17 |
| Antler-weights (lbs. & ozs.) | Year 1st . | 1·3 | 1·0 | 1·3 | 1·0 |
| | 2nd . | 5·1 | 4·3 | 3·2 | 2·15 |
| | 3rd ... | 10·1 | 7·0 | 5·15 | 4·13 |
| | 4th .. | 11·6 | 9·5 | 8·2½ | 7·1 |
| | 5th | 13·3 | 11·4 | 9·14 | 8·0 |
| | 6th | 13·5 | 11·14 | 11·3 | 9·10 |
| Maximum antler-weight (lbs. & ozs.) | | 15·14 | 16·15½ | 14·12 | — |
| Annual Increments % | 1st-2nd | 492 | 372 | 189 | 194 |
| | 2nd-3rd | 101·4 | 80·3 | 83·3 | 63 9 |
| | 3rd-4th | 14·3 | 34·8 | 41·1 | 46·8 |
| | 4th-5th | 13·5 | 21·4 | 25·7 | 13·2 |
| | 5th-6th | 1·3 | 8·3 | 15·1 | 20·3 |

In conclusion there is one point I would like to emphasize. The "normal" succession of the number of points in red deer antlers is given in all the text-books as 2—4—6—8—10—12 for the 1st to 6th antlers. From the facts at Warnham, in numerous Zoos and other parks, and also from wild stags from various geographical areas, it is quite clear that this "norm" is a very shaky one. There are many deer forests where 10 points is the normal maximum: even where 12 is the normal maximum, many individuals appear never to attain to more than 10 points. *E. g.*, Ernst R. von Dombrowski (1889) states that in Baden only about 50 per cent. become 12-pointers in their 6th year, while only about 10 per cent. ever attain to 14 points; also that in the foot-hills of the Vosges 10 points is frequently the maximum. Similar examples could also be adduced from Scotch forests. Per contra, in other conditions the succession may be much more rapid than "normal." Dombrowski (*l. c.*) states that the stags of Lower Austria in their 2nd year hardly ever show 4 points and only rarely 6, 7 points being the commonest number; while 10 or 12 points instead of 6 are frequent in 3rd year stags. Similar conditions hold at Warnham, but in even

more exaggerated form. One-year-old stags ("prickets") frequently show 4 or 6 points instead of 2, while 9 and even 11 have occurred! Similarly, in the 2nd year 4 points are never seen. In a good year 40 per cent. will have 10 to 12 points; and up to 16 points have been noted.

If, as seems to be the case, the number of points is markedly (though of course not absolutely) correlated with the absolute antler-size; and if, as also seems to be the case, absolute antler-size is an exponential function of absolute body-size (or possibly more accurately of the amount of reserves relative to absolute body-size during the period of antler-growth), these facts receive immediate explanation. The placid conditions of park existence probably permit a greater relative accumulation of reserves each year, especially in the young animals. In the wild, food conditions are again the prime factor. It would be of great interest to determine what is the normal succession of points in New Zealand stags, which, though descended from Scottish animals, may produce 20, 24 or even more points in place of 12 or 14, the usual maximum of their ancestors.

It is probable that point-number depends mainly on absolute antler-size, and that this in its turn is roughly an exponential function of body-weight. Physiologically, it is probable that it is determined chiefly by (*a*) absolute body-weight, and (*b*) relative amount of reserves. Hence annual succession of point-number depends on (*a*) rapidity of body-growth, and (*b*) conditions regulating the amount of reserves during the early period of antler-growth.

The Tables can be made to yield one further point. If the sum of the deviations in Table III. be added together for each beast (instead of for each year) and divided by the number of years for which there are records, the figure should give an indication of how much the beast's performance as regards antler-production for its whole life is above or below the average. This is given in the last column but two of Table III.

Again, I do not wish to attach too much importance to the actual quantitative results, especially in contrasting animals born at different times, and further when only a few years are available. However, it seems quite clear that marked differences between animals born in the same year, and recorded for the same length of time, must be significant. *E.g.*, JA and MA are very good performers, PA a very poor one, LA a poor one. Similarly animals with records for long series of years may be compared. We then see that E, G, N, and R were good performers, O and P very good, while A, M, and Q were poor. Also AA appears good, BA and CA poor. These individual differences may be partly due to disease, but probably are in the main determined genetically. In general, there are fewer minus deviations in the earlier years, confirming the results of Table A. This method might have advantages in deciding which stag in a park to retain for breeding if heavy horns were desired.

## Table I. (pp. 1032–33).

The weights (in lbs. and ozs. avoirdupois) of the series of shed antlers of 37 Red Deer—34 from Warnham Court, Sussex, 1 from the British Museum, 2 from German stags (Dombrowski); also the average body-weight of Scottish (Jura) Red Deer in successive years as estimated by H. Evans. 1st, 2nd, &c. year denotes 1st, 2nd, &c. year *of antler-growth.* Weights in brackets have been arrived at by allowing for weight of skull (without lower jaw). The actual weights including skull are given in the last column. The last weight for No. 1 was as estimated by J. G. Millais. "no wt." indicates that no weight is available, as the antlers are mounted on a stuffed head. The first pair of antlers of Nos. 24–33 were not taken. Nos. 18–20 and 22–33 are still alive. A weight in **thick** type indicates that this is the maximum for an animal which is no longer alive. (S) indicates that all antlers of the series were mounted on wooden shields for which 1 lb. has been allowed

## Table II. (p. 1034).

Mean annual growth of Antlers for Warnham stags (obtained from Table I.)

## Table III. (facing p. 1034).

The antler-growth of 34 Warnham stags, arranged by calendar years. The figures under each year indicate the percentage deviation (positive or negative) of the stag's antler-weight increment for that year from the average increment in antler-weight for all stags of the same age (as obtained from Table II.). b=year of birth. There is no increment (or rather, it is infinite) for the 1st year after birth. "no wt." indicates that antlers were produced but could not be weighed as they were mounted on stuffed heads. When (as is usually the case) the mean increment is positive, a negative individual deviation of $>100$ means an absolute decrease in antler-weight for that year. Similarly when (as for 11th, 12th, and 14th years of antler-growth) the average increment for all the stags is negative, a positive individual deviation of $>100$ means an absolute increase in antler-weight.

The last vertical columns give the number of years of antler-growth for which increment-figures are available; and the performance of the individual animal as regards antler-growth, as indicated by the mean percentage deviation, from the average of all its annual increments of antler-growth.

The last horizontal column but one gives the effect of the season on antler-growth, obtained by taking the mean of all the individual deviations for that calendar year. It will be seen that the mean seasonal deviation may be considerably larger than any mean individual deviation—up to $+307$ and down to $-200$ for season as against $+131$ and $-87$ for the individuals. The figures for No. 34, in the last horizontal column, arrived after the calculations had been made, and it was not thought worth while to recalculate.

| Serial No. | Designation of specimen. | 1st Year. | 2nd Year. | 3rd Year. | 4th Year. | 5th Year. | 6th Year. | 7th Year. | 8th Year. | 9th Year. |
|---|---|---|---|---|---|---|---|---|---|---|
| 1. | * ......... | — | — | — | — | — | — | — | 9·8 | 12·8 |
| 2. (S) | A .. ..... | 0·10 | 6·4 | 11·6 | 12·2 | 13·12 | 13·4 | 13·8 | 14·6 | **16·4** |
| 3. (S) | B ......... | 1·8 | 4·8 | 10·0 | 12·0 | 12·8 | 12·4 | **15·8** | 15·4 | no wt. |
| 4. (S) | C ........... | 1·0 | 4·6 | 8·12 | 10·3 | 13·4 | **(14·8)** | .. | ... | ... |
| 5. (S) | E ..... .. ... | 1·0 | 3·8 | 7·4 | 9·0 | 9·0 | 10·6 | 8·2 | 12·12 | 11·4 |
| 6. (S) | F ........... | 0·12 | 2·12 | 8·0 | 8·4 | 9·4 | 11·4 | 11·4 | 10·8 | 12·12 |
| 7. (S) | G ........... | 0·8 | 4·12 | 6·0 | 9·8 | 14·12 | 12·12 | 13·0 | 15·8 | 13·4 |
| 8. (S) | H ........... | 1·9 | 4·14 | 6·15 | 7·12 | 9·14 | **(11·6)** | ... | ... | ... |
| 9. (S) | K .......... | 1·5 | 5·0 | 6·12 | 11·15 | 13·6 | 13·12 | 16·10 | 13·6 | 17·4 |
| 10. (S) | M ........... | 2·0 | 5·8 | 7·8 | 8·4 | 10·4 | 13·5 | 13·7 | **14·0** | (12·4) |
| 11. | N ........... | 1·0 | 3·2 | 4·8 | 8·0 | 8·12 | 14·2 | 14·10 | 14·8 | 15·14 |
| 12. | O .. .... .. | 1·2 | 3·0 | 5·6 | 5·8 | 8·10 | 9·12 | 12·7 | 14·4 | 14·7 |
| 13. | P .......... | 1·0 | 3·4 | 6·2 | 6·8 | 8·8 | 8·0 | 9·14 | 10·4 | **(13·0)** |
| 14. | Q ...... .. | 0·12 | 2·9 | 5·15 | 10·0 | 9·14 | 9·12 | 11·8 | 10·14 | 11·9 |
| 15. | R .. .. .. .. | 1·5 | 2·13 | 6·3 | 10·11 | 13·4 | 12·2 | 13·15 | 13·13 | 14·8 |
| 16. | V .......... | 0·14 | 3·2 | 5·0 | 10·0 | 11·13 | 10·8 | 11·12 | 12·12 | 12·6 |
| 17. | AA ...... .. | 1·4 | 3·8 | 6·5 | 7·14 | 10·4 | 11·3 | **(13·12)** | — | ... |
| 18. | BA .. ..... | 1·4 | 3·0 | 5·12 | 8·4 | 8·8 | 11·12 | 8·14 | 9·8 | ... |
| 19. | CA .. .. .. | 0·14 | 2·4 | 6·15 | 8·0 | 7·14 | 11·8 | 9·0 | 8·0 | .. |
| 20. | DA .. .. .. | 1·1 | 2·4 | 4·7 | 6·3 | 7·0 | 10·2 | 7·8 | 8·9 | .. |
| 21. | EA ...... .. | 0·10 | 2·0 | 4·9 | 6·3 | **13·0** | (10·1) | — | .. | ... |
| 22. | FA ........ | 0·15 | 2·13 | 3·13 | 6·2 | 11·2 | 8·8 | 8·14 | ... | .. |
| 23. | GA ...... .. | 1·0 | 2·1 | 4·12 | 8·10 | 10·4 | 5·7 | 10·3 | .. | .. |
| 24. | HA . ..... | — | 2·12 | 3·9 | 7·15 | 7·3 | 8·3 | .. | . | .. |
| 25. | IA ... .... | — | 3·4 | 4·0 | 6·12 | 7·0 | 8·0 | .. | .. | ... |
| 26. | JA ...... . | — | 2·12 | 4·11 | 8·15 | 6·0 | 9·15 | . | ... | ... |
| 27. | KA ..... | — | 2·7 | 3·15 | 6·4 | 7·4 | 9·1 | | .. | .. |
| 28. | LA ... .. | — | 3·10 | 3·8 | 7·3 | 7·7 | 7·13 | .. | ... | ... |
| 29. | MA ..... | — | 3·8 | 5·4 | 5·15 | 7·7 | — | ... | .. | ... |
| 30. | NA .. . .. | — | 3·0 | 5·9 | 6·7 | 8·5 | — | .. | ... | .. |
| 31. | OA .. ..... | — | 3·4 | 4·1 | 5·1 | 7·0 | — | ... | ... | .. |
| 32. | PA ...... .. | — | 5·0 | 5·13 | 6·10 | (6·7) | — | ... | .. | .. |
| 33. | QA ...... .. | — | 2·10 | 4·12 | 7·8 | 7·14 | — | ... | ... | ... |
| 34. | Edin. .. ... | 0·12 | 3·12 | 5·0 | 8·0 | 9·12 | **10·4** | 7·4 | no wt. | |
| 35. | B.M. ......... | 0·5½ | 1·3 | 1·14 | 3·13½ | 5·10½ | 6·9 | 7·14 | 8·2 | **9·8½** |
| 36. | D 1 ......... | $n$ 15·6 | $n+1$ 17·10 | $n+2$ 17·10 | $n+3$ 17·10 | $n+4$ 13·3 | — | | | |
| 37. | D 4 ..... | 13·3* | — | 10·7 | 11·0 | 13·3 | became abnormal | | | |

**Body-weight (lbs.) of male Red Deer, Jura (H. Evans) (estimated) :—**

| | 1st Year | 2nd Year | 3rd Year | 4th Year | 5th Year | 6th Year | 7th Year | 8th Year | 9th Year |
|---|---|---|---|---|---|---|---|---|---|
| Weight ......... | 84 | 98 | 126 | 154 | 175 | 196 | 203 | 210 | 217 |
| % increase ... | — | (16·8) | (28·5) | (22·2) | (13·6) | (12·0) | (3·6) | (3·4) | (3·3) |

* Captured in snow the winter previous.

| 10th Year. | 11th Year. | 12th Year. | 13th Year. | 14th Year. | Actual weights of skull + antlers (without lower jaw). | Notes. |
|---|---|---|---|---|---|---|
| 18·8 | 16·0 | **17·0** | 16·8 | (15·4) | — | Shot, going back. |
| 14·12 | no wt. | | .. | . | — | Shot, very little sign of going back. |
| .. | ... | ... | .. | | — | Shot, going back. |
| ... | ... | . | . | .. | 17·12 | Accidentally killed. |
| **14·4** | (7·0) | ... | . | . | 9·4 | Serious lung-disease. |
| 9·8 | **13·6** | (9·8) | .. | . | 12·0 | |
| **19·4** | (12·4) | ... | . | | 15·4 | |
| .. | ... | .. | . | | 14·8 | Killed in fight with another stag. |
| **21·0** | (16·0) | ... | .. | . | 19·8 | |
| ... | .. | .. | .. | | 15·8 | |
| **16·4** | (10·10) | ... | | | 13·4 | Poor condition after eating poisonous plants. |
| 15·10 | **17·8** | (11·0) | . | .. | 13·8 | |
| ... | .. | . | ... | .. | 16·4 | |
| **(12·2)** | .. | .. | ... | . | 15·6 | |
| 17·0 | 16·12 | 16·5 | **17·9** | (16·4) | 19·8 | Died of old age. |
| **(14·6)** | .. | .. | . | . | 17·10 | Broke its back. |
| .. | ... | . | | . | 17·0 | Killed in fight with another stag. |
| . | | .. | ... | | — | Still alive. |
| ... | . | ... | . | . | — | Still alive. |
| | | .. | | .. | — | Still alive. |
| .. | | .. | ... | | 13·4 | Shot, because going back badly. |
| .. | ... | ... | ... | | . | |
| .. | | . | .. | .. | . | |
| ... | | . | . | | | |
| ... | .. | | . | .. | | |
| .. | .. | . | | . | | |
| .. | ... | . | | .. | | Still alive. |
| | . | .. | | | | |
| ... | . | . | | | ... | |
| ... | . | | | | | |
| .. | .. | .. | .. | . | | |
| ... | .. | . | .. | . | | |
| ... | ... | . | . | . | | |
| 9·4½ | 9·7 | 7·14 | (8·2) | | | |
| 227 | 234 | 238 | | | | |
| (4·6) | (8·1) | (1·7) | | | | |

## Table II.

### Mean Annual Growth of Antlers for Warnham Stags (obtained from Table I.).

[Mean total antler-weights in ounces avoirdupois.]

In (B) the arrows point from the mean weight of a given group of stags to the increment achieved by these same animals in the next year. These increments (and not those under A or C) have been taken as standard.

| Years of antler-growth..... ... | | 1st. | 2nd. | 3rd | 4th. | 5th. | 6th. | 7th. | 8th. | 9th. | 10th. | 11th. | 12th. | 13th. | 14th. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| (A) All specimens...... ..... | Number ....... | (22) | (32) | (32) | (32) | (32) | (27) | (19) | (17) | (13) | (12) | (8) | (4) | (2) | (2) |
| | Weight .... | 17·0 | 54·4 | 93·7 | 129·8 | 153·4 | 173·4 | 188·4 | 195·5 | 218·2 | 240·0 | 219·0 | 215·3 | 272·5 | 252·0 |
| | Increment %... | — | +220·0 | +72·2 | +38·6 | +18·1 | +13·1 | +8·6 | +5·2 | +10·1 | +10·0 | −8·8 | −1·7 | +26·6 | −7·5 |
| (B) All specimens for which records exist for at least 2 successive years ......... ...... | Number .... .. | — | (22) | (32) | (32) | (32) | (27) | (19) | (16) | (13) | (12) | (8) | (4) | (2) | (2) |
| | Weight ...... ... | — | 56·2 | 93·7 | 129·8 | 153·4 | 173·4 | 188·4 | 198·3 | 218·2 | 240·0 | 219·0 | 215·3 | 272·5 | 252.0 |
| | Increment % . | | +230·6 | +72·2 | +38·6 | +18·1 | +8·5 | +5·2 | +3·9 | +6·5 | +9·6 | −13·4 | −15·4 | +2·3 | −7·5 |
| | Number . . ... | (22) | (32) | (32) | (32) | (27) | (19) | (16) | (13) | (12) | (8) | (4) | (2) | (2) | |
| | Weight ........ | 17·0 | 54·4 | 93·7 | 129·8 | 159·8 | 179·1 | 190·9 | 204·8 | 219·0 | 252·8 | 254·5 | 266·5 | 272·5 | |
| (C) 11 specimens with continuous records for 10 years or more ... | Weight ........ | 16·4 | 61·6 | 107·5 | 150·2 | 178·5 | 190·5 | 203·9 | 214·8 | 220·7 | 242·2 | | | | |
| | Increment %... | — | +275·7 | +74·5 | +39·7 | +19·5 | +6·8 | +7·0 | +5·3 | +2·8 | +9·7 | | | | |

[*To face page* 1034.

| 1918. | 1919. | 1920. | 1921. | 1922. | 1923. | 1924. | 1925. | Mean annual deviation % of animal. | No. of Years | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | | | |
| | | | | | | | | −9·2 | 9 | A |
| | | | | | | | | +9·4 | 7 | B |
| | | | | | | | | +24·0 | 5 | C |
| | | | | | | | | +40·3 | 10 | E |
| | | | | | | | | +3·5 | 11 | F |
| | | | | | | | | +36·3 | 10 | G |
| | | | | | | | | +8·0 | 5 | H |
| | | | | | | | | +4·9 | 10 | K |
| | | | | | | | | −28·5 | 8 | M |
| | | | | | | | | +30·5 | 10 | N |
| −141 | | | | | | | | +75·9 | 11 | O |
| | | | | | | | | +62·4 | 8 | P |
| | | | | | | | | −11·6 | 9 | Q |
| +69 | +89 | +83 | +230 | ±0 | | | | +33·3 | 13 | R |
| ±0 | −231 | +129 | +118 | −144 | +58 | | | +9·3 | 9 | V |
| −22 | +11 | −36 | +66 | +7 | +339 | | | +60·8 | 6 | AA |
| — | −39 | +27 | +13 | −83 | +340 | −571 | +79 | −32·1 | 7 | BA |
| — | −32 | +182 | −60 | −109 | +441 | −325 | −385 | −41·1 | 7 | CA |
| — | −52 | +35 | +2 | −28 | +425 | −598 | +264 | +6·9 | 7 | DA |
| b | — | −5 | +78 | −8 | +407 | −366 | | +39·2 | 5 | EA |
| b | — | −13 | −51 | +57 | +350 | −378 | +52 | +2·8 | 6 | FA |
| b | — | −54 | +80 | +111 | +4 | −181 | +53 | +2·2 | 6 | GA |
| | b | — | — | −9 | +92 | −152 | +65 | −1·0 | 4 | HA |
| | b | — | — | −68 | +73 | −80 | +68 | −1·8 | 4 | IA |
| | b | — | — | −2 | +135 | −281 | +672 | +131·0 | 4 | JA |
| | b | — | — | −15 | +52 | −12 | +194 | +54·8 | 4 | KA |
| | b | — | — | −101 | +173 | −81 | −40 | −12·3 | 4 | LA |
| | | b | — | — | +308 | −66 | +39 | +93·7 | 3 | MA |
| | | b | — | — | +18 | −59 | +50 | +3·0 | 3 | NA |
| | | b | — | — | −65 | −36 | +123 | +7·3 | 3 | OA |
| | | b | — | — | −78 | −09 | −115 | −87·3 | 3 | PA |
| | | b | — | — | +12 | +50 | −72 | −3·3 | 3 | QA |
| −24 | −48 | +39 | +53 | −28 | +143 | −200 | +75 | Mean deviation % of year. | | |
| −54 | +55 | +31 | −40 | −664 | | ... | . | −101·5 | 6 | |

## Summary.

1. The weights of the successive pairs of antlers of 37 Red Deer, 34 from the Warnham Court herd, are recorded. 33 series are recorded for the first time.
2. The mean annual increments in antler-weight for the Warnham Court herd are as follows: (*a*) for all specimens for which data exist for 2 successive years; (*b*) for specimens for which data exist for 10 or more successive years:—

| Year...... | 1st–2nd | –3rd | –4th | –5th | –6th |
|---|---|---|---|---|---|
| (*a*) ...... | 231 | 72 | 38 | 18 | 8·5 % |
| (*b*) ...... | 276 | 74·5 | 40 | 19 | 7 % |

After the 6th year the mean increments oscillate considerably, from +10 to −15 per cent.
3. The season has a great influence on antler-weight. In some seasons (*e.g.* 1924) practically all specimens produced very poor antlers, the percentage deviation from the mean of all antler-weight increments for that year being −200 per cent.; while other seasons are very favourable, *e.g.* 1923, in which the corresponding deviation of weight-increments was +143 per cent.
4. The unfavourable conditions of 1924 caused a marked absolute decrease in antler-weight in 7th-year stags, a less marked decrease in 6th-year stags, and a slight absolute decrease in 5th-year stags. In 4th-year stags, however, though the growth was very much reduced, there was an absolute increase of antler-weight.
5. Since 1900, when the treatment of the park at Warnham with lime was discontinued, the rapidity of antler-growth has not been so great.
6. The conditions affecting antler-growth are discussed.
7. A method is given for estimating quantitatively the average performance of individual stags with regard to antler-production.
8. The number of points in 1st growth antlers at Warnham is frequently 4 instead of 2. and 9- and 12-pointers have been seen. Correspondingly high numbers for 2nd and 3rd year heads are recorded.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Huxley, J. S., 1924. "Constant differential growth-ratios and their significance." 'Nature,' Dec. 20, 1924, p. 895.

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# 53. The External Characters of *Thylacinus*, *Sarcophilus*, and some related Marsupials. By R. I. Pocock, F.R.S., F.Z.S.

(Text-figures 24–49.)

[Received June 14, 1925: Read November 16, 1926.]

Contents.



## Introduction.

Considerable attention has been paid to the structure of the hind feet and marsupium in many of the genera of Polyprotodont Marsupials, but such organs as the rhinarium and ears have been comparatively neglected. Owing, moreover, to the rarity of *Thylacinus* and to its large size, which makes preservation of the entire body in alcohol a difficult matter, the feet and other external parts have in a great measure escaped detailed description and illustration. Anatomists fortunate enough to secure fresh material from zoological gardens paid attention mainly to the muscles or other internal organs. What is true of *Thylacinus* is true also to a great extent of *Sarcophilus*; and I am not aware of any records of the examination of the external characters of *Dasyurus maculatus*, the largest of the genus, in a fresh state or preserved in alcohol.

Between 1904 and 1914 I examined in the Society's Prosectorium an adult male and female of *Thylacinus*, several adults of both sexes of *Sarcophilus*, and one adult female of *Dasyurus maculatus*; and this paper is based primarily upon my notes and

sketches taken from these specimens, supplemented by similar data yielded by examples of *Dasyurus viverrinus*, the most commonly imported of all the Australian Polyprotodonts. For information regarding the external characters of the two remaining species of Australian Dasyures, *D. geoffroyi* and *hallucatus*, and of the genera *Dasyuroides*, *Dasycercus* (=*Chætocercus*), *Phascogale*, *Sminthopsis*, *Antechinomys*, and *Myrmecobius*, I have had recourse to the spirit-preserved material in the British Museum.

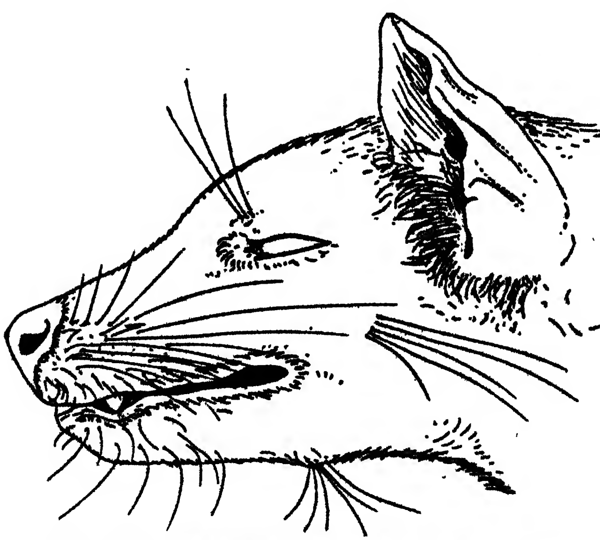
One of the main purposes I had in view in undertaking this research was to ascertain if the external characters of *Thylacinus* justify the opinion that this genus is unrelated to the Dasyuridæ, or at most remotely related to them, its kinship lying with the extinct South American Sparrasodont Marsupials as maintained by Bensley, Osborn, Gregory, and others.

## The Head and its Organs.

### *The Facial Vibrissæ.*

In 1914 (Proc. Zool. Soc. p. 891) I briefly described the facial vibrissæ of a few Polyprotodont Marsupials, including

Text-figure 24.



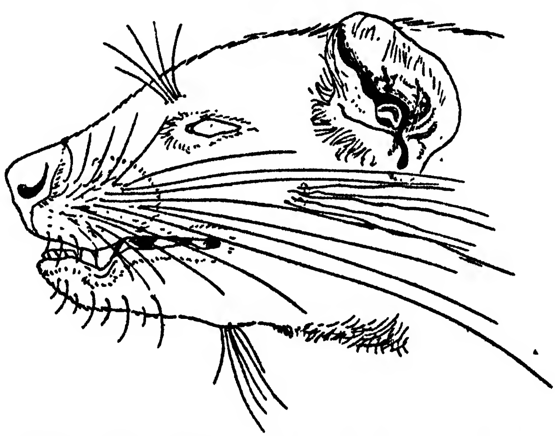
**Side view of head of *Thylacinus*, showing the facial vibrissæ.**

***Thylacinus*, *Sarcophilus*, and *Dasyurus*, and pointed out the invariable occurrence in the forms examined of the mystacial, superciliary, genal, and interramal tufts.**

In *Thylacinus* (text-fig. 24, p. 1038), as stated, the vibrissæ are relatively shorter, finer, and fewer than in the other types examined; but they vary in length individually, being sometimes longer than in the example described and figured in 1914. Nevertheless they are relatively much shorter and actually much fewer in this genus than in the smaller Australian Polyprotodonts, and show an adaptive approximation to the vibrissæ of the Canidæ, except that in the latter there are always two genal tufts of each cheek, one set high above the other. To my previous description it may be added that the lower lip is provided on each side with a well-developed series of submental vibrissæ, one of which is longer than the others.

The reduction in number and length of the vibrissæ in *Thylacinus* is to be explained, probably in connection with

Text-figure 25.



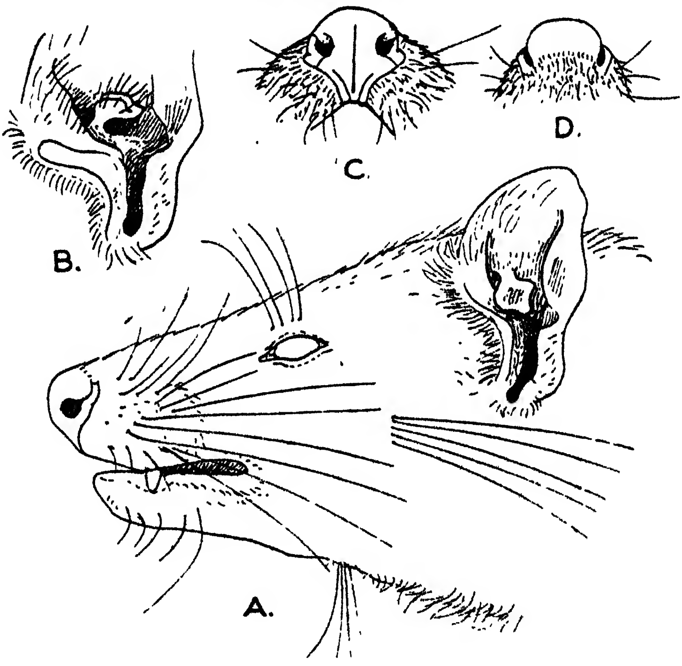
Side view of head of *Sarcophilus*, showing the facial vibrissæ.

its mode of life, as a cursorial predatory marsupial which captures its prey to a great extent by speed of foot in the open and not by stealthy creeping through thickets or in crannies of rocks, where the tactile sense of the vibrissæ would be especially useful. *Sarcophilus* shows a great contrast to *Thylacinus* in the larger number and length of the mystacial, genal, and interramal vibrissæ. The genal tuft is particularly well developed, the numerous vibrissæ, a dozen or more, rising often from a nearly naked subcircular area of skin, most of them being so long that their tips reach back well beyond the ear and lie alongside the fore part of the neck. The mystacials are correspondingly long and, like the genals, are comparatively rigid and frequently sinuous in this course. (Text-fig. 25.)

From the subjoined figure of the head of *Dasyurus maculatus* it

may be seen that the vibrissæ are similar to those of *Sarcophilus*, and in all the genera and species of Dasyuridæ examined I found the tufts of vibrissæ constant in occurrence and position, the only variations being in the number and length of the bristles. By way of illustration I have figured those of *Antechinomys spenceri*. (Text-fig. 32, A, p. 1048.)

Text-figure 26.




A. Side view of head of *Dasyurus maculatus*, showing the facial vibrissæ and the ear with the valvular supratragus lowered.

B. Base of ear of the same with the supratragus raised.

C. Rhinarium of the same from the front.

D. The same from above.

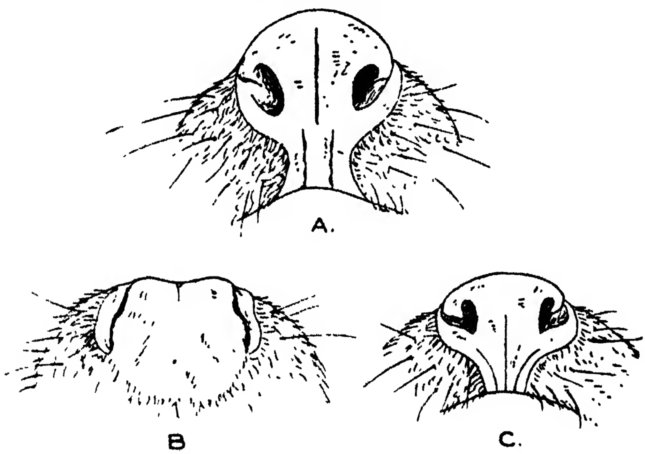
In *Myrmecobius*, however, some differences are noticeable. The mystacial vibrissæ are greatly reduced in number and length, as is always the case in anteating mammals; and the sides of the muzzle and the lips are nearly naked. There are two short and slender superciliary bristles; but the genal tuft, rising from a small tubercle, is more in evidence, and consists of some half-dozen bristles of moderate length. The interramal tuft is

altogether suppressed—a unique feature in the Australian Polyprotodonts. (Text-fig. 32, B, p. 1048.)

### *The Rhinarium.*

The *Rhinarium* in *Thylacinus* is large, coriaceous, entirely naked, and sometimes projects prominently beyond the edge of the upper lip, towards which its anterior surface then recedes downwards and backwards. Viewed from above, its upper surface is about one-fourth wider than long, its anterior edge is lightly emarginate, its posterior edge ill-defined from the integument behind it, its lateral edges behind the nostrils are convex, and only a small area of the nostrils is exposed. In profile view the nostrils are large and open outwards and forwards. Viewed from the front it is about as wide as high, but the inferior third of it is constricted to

Text-figure 27.

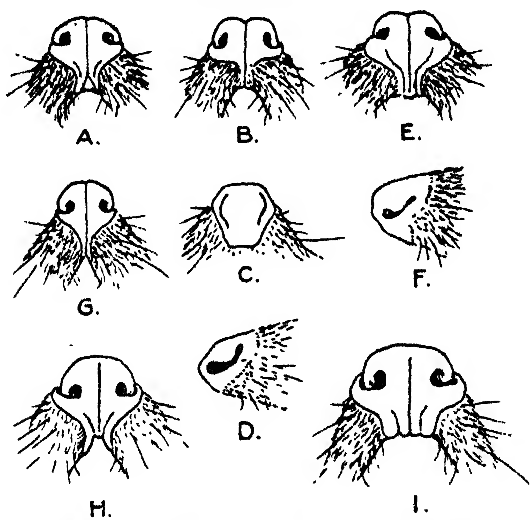



A. Rhinarium of *Thylacinus* from the front.
B. The same from above.
C. The same of *Sarcophilus* from the front.

form a very definite philtrum about as wide as high with nearly vertical sides defined by the hair of the upper lip. This philtrum is marked by a pair of vertical parallel grooves, one on each side of the middle line, which do not ascend as high as the nostrils. The upper edge is strongly convex from side to side, and the internarial space is wide and marked by a median vertical groove, which does not reach the summit of the upper surface above and ceases below on a level with the upper ends of the grooves of the philtrum. There is a tolerably deep infranarial area on each side. (Text-fig. 27, A, B).

In *Sarcophilus* the rhinarium is large and naked as in *Thylacinus*, but is somewhat different in shape. Seen from the anterior aspect, it is wider as compared with its height, being flatter along its upper edge and having a shorter philtrum. The median groove does not extend above so high as the upper edge of the nostrils, but inferiorly it reaches to the lower edge of the philtrum, being deep and wide at its lower end. As in *Thylacinus*, the philtrum is marked with a pair of grooves, in addition to the

Text-figure 28.




A. Rhinarium of *Phascogale penicillata* from the front.
B. The same of *P. lorentzi*.
C. The same from above.
D. The same from the side.
E. The same of *P. wallacei* from the front.
F. The same from the side.
G. The same of *Antechinomys spenceri* from the front.
H. The same of *Dasycercus*.
I. The same of *Didelphys marsupialis azaræ*.

median groove, but instead of being erect and parallel, they diverge as they pass upwards, running parallel to the adjacent outer edge of the philtrum and of the area of the rhinarium above it. The infranarial portion of the rhinarium is defined in front by a faint groove. Seen from above the anterior edge is nearly straight from side to side, is lightly convex, not mesially emarginate as in *Thylacinus*. (Text-fig. 27, C, p. 1041.)

In *Dasyurus maculatus* the rhinarium is very similar to that of *Sarcophilus* in shape and is similarly grooved (text-fig. 26, A, C,

p. 1040); and the same may be said of *D. viverrinus*, *geoffroyi*, and *hallucatus*, of which there are specimens in the Natural History Museum preserved in alcohol.

In *Phascogale** the rhinarium is variable. In some of the species, such as *P. wallacei* and *P. thorbeckiana*, the philtrum, although short, is broad, and its deep median groove is continued upwards to the summit of the anterior face of the rhinarium and its lateral grooves, parallel with the median groove and the lateral margins of the philtrum, diverge above and extend almost up to the nostrils. In *P. penicillata* the anterior face of the rhinarium is also grooved throughout, but inferiorly on the philtrum it bifurcates, defining a median triangular wedge, very much as in some specimens of *Sarcophilus*. The lateral grooves are very short, faint, and incomplete. In *P. lorentzi* the philtrum is almost obliterated. The median groove extends to the edge of the lip, but on each side of it the remains of the philtrum are very obscurely indicated. The partial suppression of the philtrum, foreshadowed in *P. lorentzi*, and possibly in other species of the genus, is repeated further in *Antechinomys spenceri*, which has a particularly shrew-like snout, the rhinarium having a mesially sulcate philtrum without lateral grooves.

In the genera *Dasyuroides*, *Dasycercus* (*Chætocercus*), and *Sminthopsis* there is nothing particular to note about the rhinarium, which shows a close resemblance to that of the other Australian genera mentioned above; and it may be recorded in passing that the rhinarium of *Didelphys marsupialis* differs only in minor details from that of *Sarcophilus* or *Dasyurus*. And since the Didelphyidæ were doubtless the primitive stock which gave rise to the Dasyuridæ, the type of rhinarium seen in *Dasyurus* and *Sarcophilus* may be safely regarded as the most primitive type in the family to which they belong, the aberrant rhinaria of *Thylacinus*, of some species of *Phascogale* and of *Antechinomys* being comparatively simple modifications of that type. (Text-fig. 28, A–I, p. 1042.)

In the only example of *Myrmecobius* available for examination the rhinarium is distorted by crushing and its details obscured. But so far as can be seen, it does not differ essentially from that of the Dasyuridæ.

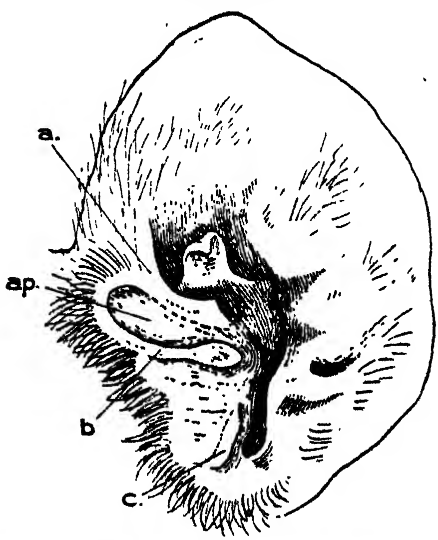
*The Ear.*

The ear in *Thylacinus* is moderately large; its height exceeds its antero-posterior width and it is attached to the head by a broad base. Its anterior edge is lightly convex up to the somewhat narrowed apex, and from the apex to its inferior point of attachment the margin is more strongly but less regularly convex. Nowhere is the edge overfolded, and when the ear is expanded and flattened there is a large laminate area above and

* More detailed study than has as yet been possible of the rhinarium, ears, and other external characters of the numerous species assigned to this genus will probably yield interesting results of some systematic importance.

behind the cavity and a narrower but conspicuous area in front of the upper end of the cavity. The cavity is deep. Its upper portion carries a well-developed, valvular supratragus (*plica principalis* of Boas). This is normally directed downwards and outwards, and is more or less folded, or bent, on itself. Below and in front of this there is a strong, sharp-edged, upstanding, crescentically-curved ridge which forms the boundary of the upper portion of the cavity and, curving downwards below the level of the supratragus, ceases in an obliquely cut away edge. This ridge forms the upper margin of a perfectly smooth, antero-posteriorly elongated area which is bordered below by a thickened

Text-figure 29.

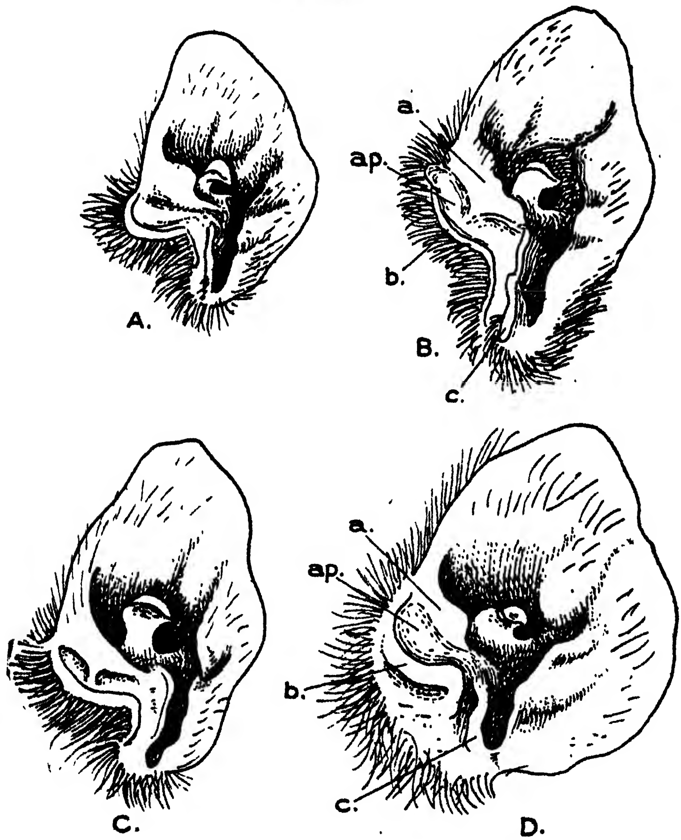



Ear of *Thylacinus* expanded with the supratragus raised. *a*. The anterior ridge; *ap*. the anterior passage which is capable of being closed by the raising of the ridge *b* against *a*; *c*. ridge strengthening the border of the inferior passage or cleft in front of the auditory orifice.

ridge ending in a clavate expansion below the posterior end of the upper ridge and at the upper anterior end of the cartilaginous wall which bounds in front the lower portion of the ear-cavity. The two ridges above described (text-fig. 29, *a* and *b*) are fringed with hairs overlapping the smooth area which, running between the two grooves and opening posteriorly into the cavity of the ear and anteriorly to the exterior, acts probably as a passage for sound. It may be called the anterior passage (*ap*). The lower portion of the ear-cavity is deep, and forms exteriorly a long, vertical cleft capable of being expanded or contracted to

a narrow slit by the separation or juxtaposition of its anterior and posterior walls. The anterior wall is strengthened below by a short, thick, cartilaginous crest (*c*) lying on the lower part of a naked area of skin which extends in front of the cleft and

Text-figure 30.




A. Ear of *Dasyurus geoffroyi.*
B. The same of *D. viverrinus.*
C. The same of *D. hallucatus.*
D. The same of *Sarcophilus.*
Lettering of B and D as in text-fig. 29.

is bounded above by the clavate ridge (*b*). The auditory orifice opens at the bottom of the cleft, just within its anterior margin. The posterior edge of the cleft seems to represent the antitragal ridge of the ear of higher mammals, the bottom of the cleft the

intertragal notch and the anterior wall, or perhaps only its lower portion, the tragal thickening.

The cavity of the ear is capable of being closed by the folding down of the supratragus, by the narrowing of the anterior passage by the downward movement of the upper ridge ($a$) on to the lower ridge ($b$), by the juxtaposition of the anterior and posterior walls of the cleft, and by the folding of the laminate portion of the pinna along lines represented by grooves running backwards from the cavity. (Text-fig. 29, p. 1044.)

The ear of other genera of Dasyuridæ resembles in all essentials that of *Thylacinus*. In *Sarcophilus* the laminate areas above and behind the cavity are relatively a little more extensive; ridge $a$ is developed into a semicircular valvular flap, supplementing the twisted supratragal flap in closing the cavity; ridge $b$ is thicker throughout its length and not markedly clavate posteriorly; and the tragal ridge ($t$) is continued upwards along the anterior edge of the inferior cleft to terminate behind the posterior end of ridge $b$ and beneath the posterior end of ridge $a$, and is defined throughout its length in front by a tolerably deep groove. (Text-fig. 30, D, p. 1045.)

In the species of *Dasyurus* there are some interesting variations in the ear. The inferior laminate portion behind the inferior cleft is much narrower than in *Sarcophilus*, narrower even than in *Thylacinus*. In *D. viverrinus** ridge $a$ is sinuously folded and attached by a strand to the floor of the anterior passage; ridge $b$ is narrow and posteriorly is continued inferiorly to a point on a level with the lower margin of the inferior cleft, leaving a wide naked space between it and the ridge defining the inferior cleft in front. (Text-fig. 30, B, p. 1045.)

The ear of *D. maculatus* seems to be like that of *D. viverrinus*. (Text-fig. 26, A, B, p. 1040).

In *D. hallucatus* ridge $a$ is more evenly concave, like that of *Thylacinus*. Ridge $b$ is thicker than in *D. viverrinus* and sharply curved at its posterior end, but does not extend so far inferiorly; the anterior ridge of the inferior cleft is less well defined below and the supratragus is large to compensate possibly for the emargination of ridge $b$. (Text-fig. 30, C, p. 1045.)

In *D. geoffroyi* ridge $a$ is lobate and is not tied by a strand to the anterior passage, and ridge $b$ is very narrow where it curves inferiorly behind. In these respects it shows resemblance to the ear of *Sarcophilus*. (Text-fig. 30, A, p. 1045.)

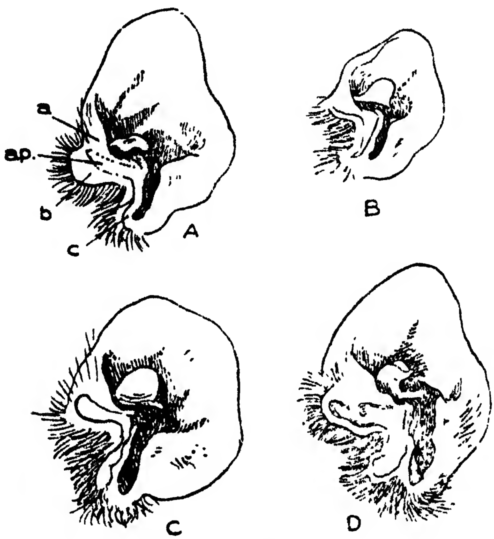
In *Dasyuroides byrnei* the ear is in essential details like that of *D. viverrinus*, but the inferior end of ridge $b$ curves backwards below and fuses with the ridge defining the anterior border of the inferior cleft (text-fig. 31, D, p. 1047). In *Dasycercus cristicauda* the ear is very similar to that of *Dasyuroides*, showing differences of only minor importance.

* The greater length of the inferior portion of the ear shown in my picture of that organ in this species is possibly due to the figure having been drawn from a spirit specimen from which the skull had been extracted.

In *Phascogale* the ear is similar to that of the genera and species above described, but it exhibits specific variations calling for further study. In *Ph. penicillata* ridge *a* is without marked lobate expansion, the supratragus is folded as in *Dasyurus* and *Thylacinus*, and ridge *b* is expanded and laminate. In *Ph. minutissima* the anterior edge of the pinna is more over-folded, the supratragus is not folded, and ridge *b* descends inferiorly. (Text-fig. 31. A, B.)

In *Phascogale lorentzi* the supratragus also forms a tolerably large, nearly semicircular flap, which is flat and unfolded and

Text-figure 31.




A. Ear of *Phascogale penicillata*.
B. The same of *P. minutissima*.
C. The same of *P. lorentzi*.
D. The same of *Dasyuroides byrnei*.
Lettering of A as in text-fig. 29.

has an evenly convex free margin. Ridge *a* has no marked lobate expansion, its edge being lightly concave as in *D. hallucatus*, and, as in that species, ridge *b* curves downwards in front of the inferior cleft, without forming quite so pronounced a crest. The laminate portion of the pinna behind the inferior cleft is expanded as in *Sarcophilus*.

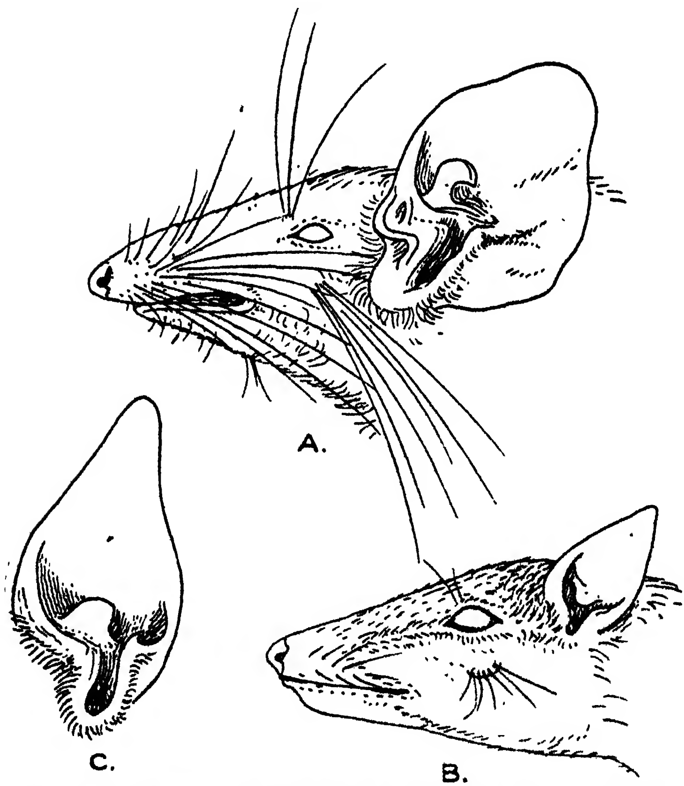
I have not examined the ears of all the species referred to *Phascogale*; but that of *Ph. calura*, described and figured by Boas *, resembles tolerably closely that of *Ph. lorentzi* (text-fig. 31, C).

* Die Ohrknorpel etc. p. 44, pl. xviii. fig. 174 (1912).

The ear of *Sminthopsis* is also of a similar type, as is shown, although somewhat obscurely, by Thomas's* figure of the ear of *S. leucopus*.

The more specialized genus *Antechinomys* also retains a typically Dasyurine ear. In *A. spenceri* it is relatively very much larger than

Text-figure 32.




A. Side view of head of *Antechinomys spenceri* showing the facial vibrissæ and the ear expanded.

B. The same of *Myrmecobius fasciatus*.

C. Ear of the same on a larger scale.

in the genera and species previously described. Ridge *a* is long and has a tolerably deeply concave edge; the supratragus is large, hooked and folded; ridge *b* has a sigmoid curvature, its posterior end curving downwards over the naked area as in *Phascogale lorentzi* and *Dasyurus hallucatus*, but its anterior end similarly

* Cat. of Marsupials, pl. xxiii. fig. 5 (1888).

bends upwards, bordering the anterior passage, and there is a small vertical cartilaginous ridge descending from the outer surface of ridge *a* to the floor of the anterior passage as in *Dasyurus hallucatus*. The naked area in front of the inferior cleft is large and the laminate area behind the cleft is expanded. (Text-fig. 32, A, p. 1048.)

In *Myrmecobius* the ear differs in some points from that of the genera above described, and is less complex in type. It is long and narrowed to a point at the summit. Ridge *a* is long, with an evenly concave free edge; the supratragus is tolerably large and valvular, unfolded with a strongly convex free margin almost as in *Phascogale lorentzi*; but ridge *b* and the anterior passage are practically suppressed, there is scarcely a trace of the naked area in front of the inferior cleft, the hairs spreading up to the tragal ridge, the antitragal lobe is bluntly rectangular, there is no definite laminate expansion behind it, but just within its upper edge there is a little pocket-like depression. (Text-fig. 32, B, C, p. 1048.)

## *The Feet.*

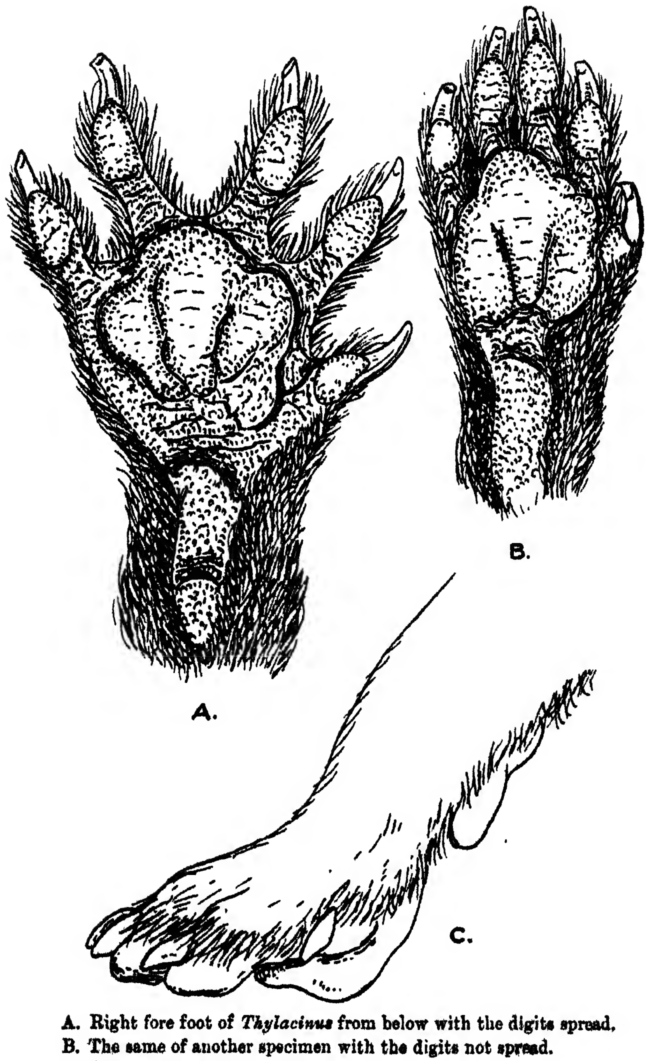
The feet of *Thylacinus* have often been likened to those of dogs. The resemblance is superficial only. In the dog's feet, digits 2 to 4 are united to the proximal end of the digital pads by webs with a thickened margin of elastic tissue which tends to hold the digits together and to strengthen the foot for swift running. The plantar pad is smaller, differently shaped and deeply emarginate behind, and the sole is hairy up to its margins. In the fore foot the ulnar carpal pad is an isolated excrescence surrounded by hair, and the first digit (pollex) is set high above the second. In the hind foot there is no trace of metatarsal pads, the whole metatarsal area being covered with hair.

As may be seen in the living animal and as shown by Scott's figure of the imprint of the foot (Proc. Zool. Soc. 1872, p. 355), *Thylacinus* is digitigrade, the feet resting upon the anterior part of the plantar pad and the digital pads, with the carpal and metatarsal pads raised from the ground. The plantar and digital pads are thickly covered with fine pointed papillæ.

## *The Fore Foot.*

In the *fore foot* of *Thylacinus* the digits are short, naked beneath, and free from webbing almost as far as the plantar pad. The digital pads are well defined and tolerably regularly oval in shape, and the area of the under side of the digits behind them in the case of digits 2 to 4 is about equal to the length of the pads. The claws are moderately long, strong, blunt, and but little curved. Digits 1, 2, 3, and 4 are tolerably evenly spaced, digit 1 being closer to digit 2 than in typical digitigrade Carnivora. The plantar pad is large, thick, soft, and cushion-like. Its distal margin is trilobed, the median lobe being the largest and projecting

Text-figure 33.

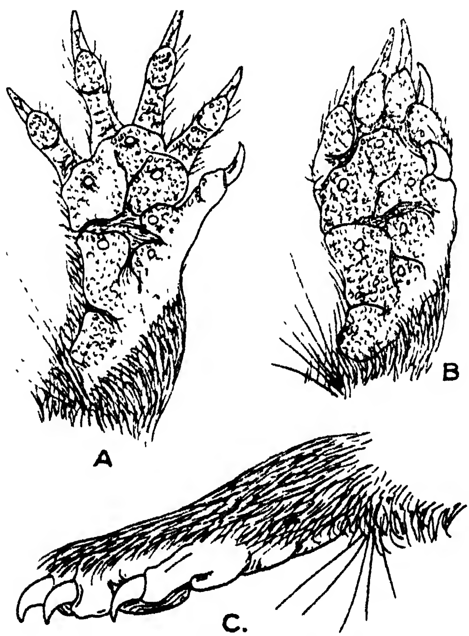



A. Right fore foot of *Thylacinus* from below with the digits spread.
B. The same of another specimen with the digits not spread.
C. The same from the inner side.

prominently beyond the laterals. The surface of the pad is impressed, at least in its proximal half, with faint grooves marking the divisional lines between its confluent elements. The pollical lobe is distinguishable, but is fused to the rest of the pad. The

skin all round the pad is naked, and appears to be glandular in the crease between the pad and digits 2 to 4. Immediately behind the pad there is a tolerably long area of naked skin gradually narrowing proximally to the carpal pad and marking the joint in the sole between the plantar and the carpal pad. The latter, representing the ulnar carpal element alone, lies nearly directly behind the middle of the plantar pad and is long and narrow, rather more than twice as long as wide. Its distal end is

Text-figure 34.




A. Right fore foot of *Sarcophilus* from below with the digits spread.
B. The same with the digits not spread.
C. The same from the inner side.

elevated and conical, and its proximal end is defined by a transverse furrow. The lower side of the carpal region of the foot is covered with hair up to the margins of the carpal pad. The carpal vibrissæ are suppressed. (Text-fig. 33, p. 1050.)

In *Sarcophilus* the fore foot is not specialized for digitigrade gait, at least the whole of the plantar pad resting on the ground; and the integument of the pads instead of being finely papillate is covered with rather coarse squamous tessellation. Digits 2 to 4 are arranged and spaced as in *Thylacinus*, but are relatively

longer, less hairy, and have longer, sharper claws. Digit 1, however, is very much longer, showing no trace of the abbreviation so noticeable in *Thylacinus*, and it is entirely naked on its outer (preaxial) surface. The plantar pad is less cushion-like, but is rather wider as compared with the width of the foot and with its own length. Its main portion is more distinctly trilobed, the lateral lobes projecting more prominently at the sides than in *Thylacinus*; and the pollical lobe, in accordance with the better-developed 1st digit, is very distinctly defined, but it lies entirely upon the proximal side of the inner of the three main elements of the plantar pad. It is noticeable that each of these four elements constituting the plantar pad carries a larger submedian scale, marking the central points of the primitive interdigital pads before their fusion to form the composite pad. The joint between the carpal and plantar pads is a deep, transverse, narrow groove, so that even when the foot is extended the carpal and plantar pads are separated only to a comparatively small extent, not to a considerable extent as in *Thylacinus*.

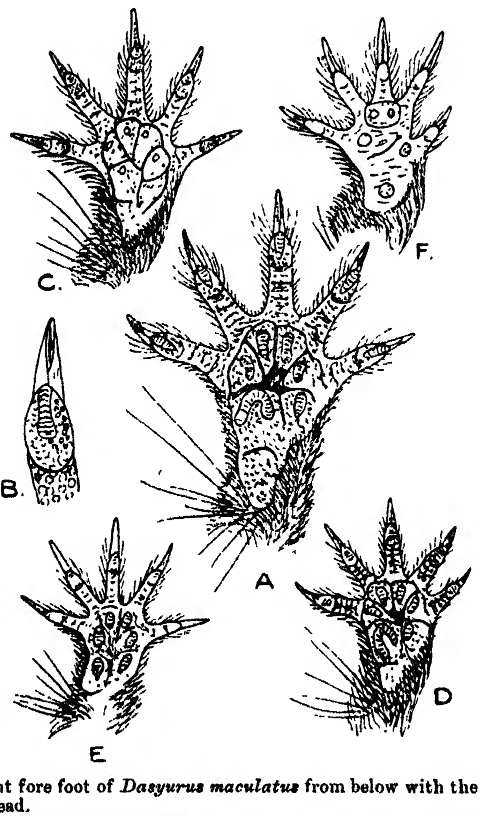
The naked carpal area is as broad distally as the plantar pad and longer, not narrower and shorter as in *Thylacinus*. Proximally it is narrowed on the inner (preaxial or pollical) side of the foot by the encroachment of hair from the carpus; but there is no similar encroachment on the outer (postaxial) side as there is in *Thylacinus*, its outer edge extending to the margin of the foot. It is incompletely divided into three areas, two distal, the carpal pads, adjoining the plantar pad and separated by a median longitudinal posteriorly-abbreviated sulcus, and a proximal defined from the outer carpal pad by a transverse, internally-abbreviated sulcus running inwards from the outer margin and representing the groove on the carpal pad of *Thylacinus*; but this outer (postaxial or ulnar) element of the naked carpal area lies on the outer side of the foot, not in the middle line as in *Thylacinus*. The two carpal elements of this area have a larger scale differentiated from the squamous tessellation, as in the case of the four elements of the plantar pad. The carpal vibrissæ are represented by a tuft of long hairs rising just on the proximal side of the termination of the naked carpal area. (Text-fig. 34, p. 1051.)

The fore foot of *Dasyurus viverrinus* * (text-fig. 38, A, p. 1059) resembles in essentials that of *Sarcophilus*; but there is a small weakly-striated area at the tip of the digital pads; the external surface of the first digit is not naked, and the four elements of the plantar pad are much more sharply defined by complete grooves and the pollical element is relatively larger, approximately as large indeed as the rest. As in *Sarcophilus*, there is a long and wide naked area extending back to embrace the pisiform prominence, almost reaching the carpal vibrissæ.

* Figured by Wood-Jones, apparently from a dried skin ('The Mammals of S. Australia,' i. p. 90, 1923).

The fore foot of *D. geoffroyi* is similar to that of *D. viverrinus*, but the area behind or on the proximal side of the carpal pads is shorter and narrower, more triangular, and does not reach the pisiform prominence. (Text-fig. 35, C.) The fore foot of

Text-figure 35.




A. Right fore foot of *Dasyurus maculatus* from below with the digits spread.

B. Tip of digit of the same showing the striated area and the granulation behind the pad, for comparison with text-fig. 38, E.

C. Right fore foot of *D. geoffroyi* from below with digits spread.

D. The same of *D. hallucatus*.

E. The same of *Phascogale lorentzi*.

F. The same of *Myrmecobius*.

*D. maculatus* is like that of *D. viverrinus* and *geoffroyi*, except that the striated area on the digital pads is larger and more completely striate, and that the lobes of the plantar pad and the carpal pads are provided each with a large very definite

striated area, the area on the outer or ulnar carpal pad being crescentically curved or horseshoe-shaped. As in *D. viverrinus*, the naked area behind the carpal pad extends proximally almost to the carpal vibrissæ. (Text-fig. 35, A, B, p. 1053.)

*Dasyurus hallucatus* has a fore foot like that of *D. maculatus*, except that the entire lower side of the digital pads is striated, transversely at the apex, as in *D. maculatus*, and longitudinally behind, and also in the pairing and large size of the tubercles on the under side of the digits behind the digital pads (text-fig. 35, D, p. 1053).

*D. albopunctatus*, of which I have only seen dried skins, seems to have a foot similar to those of *D. maculatus* and *geoffroyi*.

In *Phascogale* the fore foot resembles tolerably closely in general form and proportion those of *D. maculatus* and *hallucatus*, having striated areas on the pads; but the four elements of the plantar pad are more primitive in disposition in that they do not coalesce to the same extent to constitute a large continuous plantar pad. The posterior part of the sole, moreover, is relatively shorter and wider, and not so markedly narrowed by encroachment of hairs from the wrist on the inner or preaxial side. Typically both the carpal pads are retained and represented by striated areas, that of the inner pad being almost always horseshoe-shaped as in *D. maculatus* and *hallucatus*, although sometimes it is merely hooked at the end and sometimes (*Ph. lorentzi*) simply oval, as shown in the figure (text-fig. 35, E, p. 1053). Hence in these species there are six distinct pads on the sole; but in a few species, e.g. *Ph. swainsoni* and *minima*, as noticed by Thomas, the inner carpal is not distinct *.

In *Dasyuroides byrnei* the fore foot is generally similar to that of *Dasyurus*, but the sculpturing is relatively coarser, and the median areas of the pads are large and very finely striolate. The foot of *Dasycercus cristicauda* has small, oval, smooth central areas on the plantar and carpal pads, but otherwise differs in no essential respects from that of *Dasyuroides*. In both of these genera the central area of the external carpal pad is like the rest, and not hooked or crescentically curved.

The fore foot of *Sminthopsis* shows no features of special interest, being very like that of *Phascogale*, even in the retention of the horseshoe-shaped striated carpal area, at least in some species; but that of *Antechinomys spenceri* is elongated, especially in the carpal region, there being a long naked or nearly naked tract behind the outer carpal pad running back to the origin of the carpal vibrissæ, which are very long. The inner carpal pad is suppressed, and so also is the pollical lobe of the plantar pad in the specimen examined. Thus the plantar pad is three-lobed,

* Thomas in his Catalogue described the pollical pad as divided when the inner carpal pad is present, and as undivided when it is absent. The inner carpal pad is, however, a distinct element from the pollical lobe of the plantar pad. Wood-Jones's figure of the fore foot of *Ph. flavipes* clearly shows the horseshoe-shaped striated area on the external carpal pad.

and each lobe, like the single carpal pad, carries a small smooth circular area. (Text-fig. 39, A, p. 1061.)

Assuming the fore foot of *Phascogale* to represent the primitive type amongst the Australian Polyprotodonts, the fore feet of *Dasyurus maculatus* and *hallucatus* are easily derivable from it. From the latter can be derived the type of fore foot found in *Dasyurus geoffroyi* and *D. viverrinus*, and from the latter it is but a step to the fore foot of *Sarcophilus*. The fore feet of *Dasyuroides* and *Dasycercus* have no doubt had an origin similar to that of *D. viverrinus* and *D. geoffroyi* in accordance with the adoption of terrestrial habits, and the fore foot of *Antechinomys* is a modification of that of *Sminthopsis*, which is itself derived from the foot of *Phascogale*.

From the foregoing descriptions it may be seen that the fore foot of *Thylacinus* differs from that of the other genera discussed in the following points:—

(1) The pads are thickly covered with fine pointed papillæ instead of with coarsely granular or squamous tessellation.
(2) Digits 2 to 5 are relatively a little shorter and have blunter, less compressed claws.
(3) The pollex is much shorter and the pollical lobe of the plantar pad is not so clearly distinguishable.
(4) There is a longer membranous space between the plantar pad and the carpal pad.
(5) The naked carpal area is reduced by the encroachment of hairs on each side from the wrist, and is represented only by the postaxial (ulnar or outer) element of that area: and this lies nearly in the middle of the lower surface of the foot, not on its outer half.
(6) The carpal vibrissæ are absent.

All these differences appear to be associated with the digitigrade gait of *Thylacinus*; but the reduction of the pollical lobe of the plantar pad and the fusion of its remaining three lobes are foreshadowed in *Sarcophilus*, and the constriction of the naked carpal area is foreshadowed in *Dasyurus*. *Antechinomys*, a digitigrade type, also shows suppression of the pollical lobe of the plantar pad and of the internal carpal pad and constriction of the proximal naked carpal area similar to that of *Thylacinus*.

*Myrmecobius* has a very different type of fore foot from that of any of the genera described above. As in them it is pentadactyle, but the 1st digit or pollex is quite short and separated by a long space from the 2nd. The 2nd, 3rd, and 4th are close together, equally spaced, and set in a straight transverse line, and the 3rd digit is slightly shorter than the 2nd or 4th, which are subequal. The 5th digit is about as large as the 4th, but is separated from it by a much longer space than the 4th is from the 3rd, and rises from the outer side of the foot nearly on a level with the pollex on the inner side. The claws on digits 2 to 4 are long and fossorial.

The skin of the pads and sole is smooth and wrinkled, not roughened. At the base of digits 2 to 4 there is a single transversely oblong thickened pad resulting from the fusion and expansion of the two interdigital pads, the summits of which persist as a pair of rounded discs. The two remaining interdigital pads are quite distinct and lie respectively opposite the angle between digit 1 and digit 5 respectively, the pollical element being a little behind the level of the other. Behind the pollical pad there is a naked carpal area narrowing proximally and carrying near its extremity a single rounded carpal pad, set near the middle of the foot and representing the inner (ulnar or postaxial) carpal element. (Text-fig. 35, F, p. 1053.)

Thus the fore foot of *Myrmecobius* differs much more from the Dasyurine type of fore foot than does that of *Thylacinus*. In the Dasyurine foot, and in *Thylacinus*, digits 2 to 5 are subequally spaced and digit 3 is slightly longer than digit 2, the converse being the case in *Myrmecobius*.

### *The Hind Foot.*

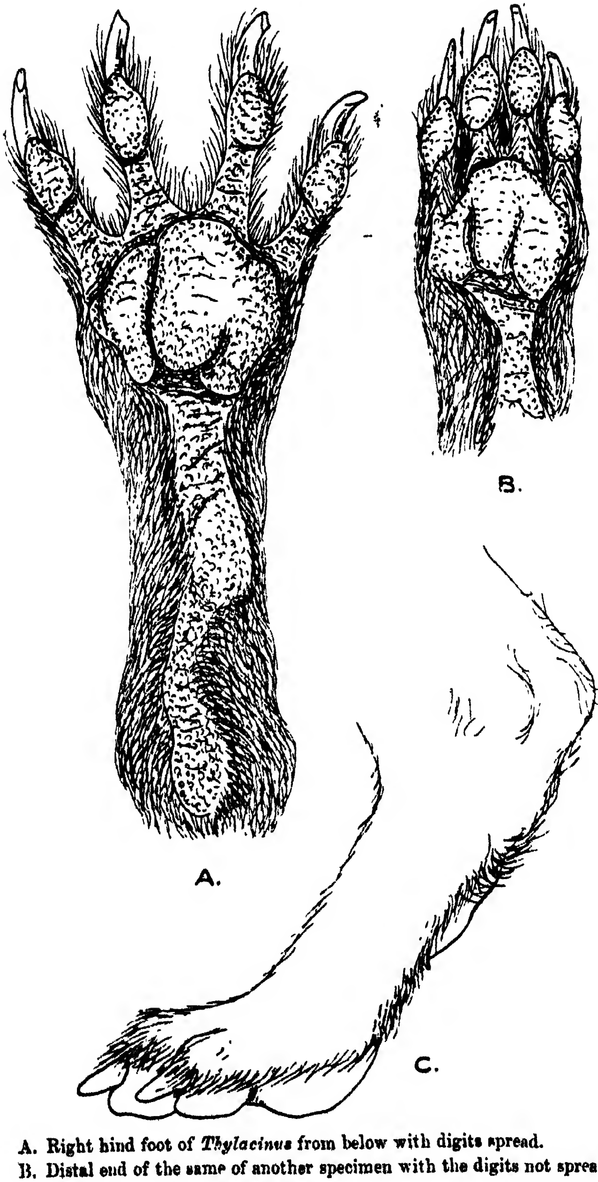
The *hind foot* of *Thylacinus* in the nakedness of the lower sides of the digits, the absence of webbing, and the development of the plantar pad resembles the fore foot; but digit 1 is entirely suppressed, digits 2 to 5 are a little longer, and form a straighter line proximally where they project beyond the distal margin of the plantar pad, which is less strongly curved. This pad is obscurely divided into three elements, at all events proximally by grooves, and its posterior margin is irregularly trilobate. Like the plantar pad of the fore foot, it is almost as wide as the foot.

The tarso-metatarsal area is naked at least along the middle line up to the tip of the hock or calcaneum; but this naked area is very irregular in shape. Its outer, postaxial or fibular, margin is sinuous from the plantar pad to the hock; its inner, preaxial, edge forms a well-marked convex bulge almost reaching the margin of the lower side of the foot, and between this and the hock there is an edge exhibiting a deep and long emargination. There is no definite trace of pads on this naked tarso-metatarsal area, and its narrowness and irregularity of outline result from the encroachment of hairs from the sides of the foot on to its lower surface. (Text-fig. 36, p. 1057.)

In *Sarcophilus** the hind foot, in accordance with the general reduction in size of the hind as compared with the fore quarters in this animal, is smaller as compared with the fore foot than in *Thylacinus* or any other Polyprotodonts, and its granulation is coarser and more squamate than in *Thylacinus*, but in the length and disposition of the digits, the absence of the hallux and the thick obscurely divided plantar pad it is very similar to

* An indifferent figure of the hind foot of a young example of this species was published by Bensley (Tr. Linn. Soc. (2), ix. 1903).

Text-figure 36.

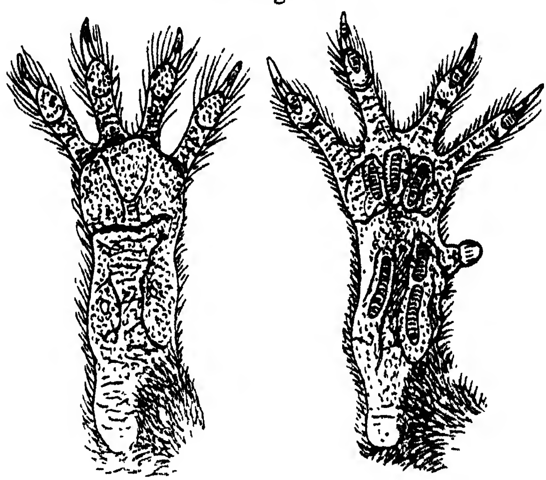



A. Right hind foot of *Thylacinus* from below with digits spread.
B. Distal end of the same of another specimen with the digits not spread.
C. The same from the inner side.

that of *Thylacinus*. The plantar pad, however, is relatively wider and is not narrowed behind, its posterior border being nearly straight; and the metatarsal area is entirely naked, the hair only encroaching upon it posteriorly on the inner side of the calcaneum. It exhibits a longish wide inner pad reaching almost from the plantar pad to the hairy patch by the heel, and a shorter but equally wide outer pad separated from the inner pad by a narrow space. (Text-fig. 37, A.)

In *Dasyurus viverrinus* the hind foot * resembles in general features that of *Sarcophilus*, but is longer and thinner, indicating an animal with much greater activity, and has the three lobes

Text-figure 37.



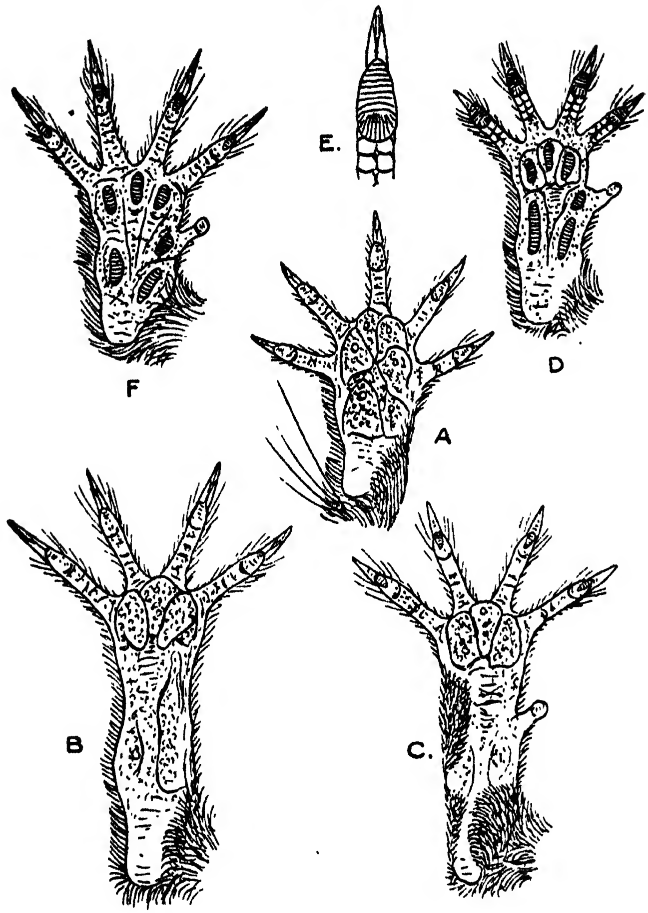

A. Right hind foot of *Sarcophilus* from below with the digits spread
B. The same of *Dasyurus maculatus*.

of the plantar pad sharply defined by two proximally convergent grooves and the digital pads tipped with a small transversely-striated area. Similar areas are present on the digital pads in all the species of *Dasyurus*; but *D. viverrinus* is the only species of the genus resembling *Thylacinus* and *Sarcophilus* in the suppression of the hallux. (Text-fig. 38 B, p. 1059.)

In *D. geoffroyi* the hind foot † resembles that of *D. viverrinus* and of *Sarcophilus* in the uniform squamous granulation of its lower surface; but differs in the retention of the hallux, which is situated near the middle of the inner edge of the sole a considerable distance away from the plantar pad. There is,

* Figured by Waterhouse, Bensley, and Wood-Jones.
† Figured by Thomas.

Text-figure 38.




A. Right fore foot of *Dasyurus viverrinus*.
B. Right hind foot of the same.
C. The same of *D. geoffroyi*.
D. The same of *D. hallucatus*.
E. Tip of digit of same showing striation of pad and paired scales behind it to compare with text-fig. 35, B.
F. Right hind foot of *Phascogale lorentzi*.

however, no hallucal pad. The metatarsal pads are not so well defined as in *D. viverrinus*, and on the outer side there is a marked encroachment of hair on the sole, not so extensive as in *Thylacinus* but similar. (Text-fig. 38, C.)

In *D. maculatus* the hind foot is stouter than in *D. viverrinus*

and *D. geoffroyi* and, as in the latter, the hallux is retained; but it rises considerably closer to the plantar pad, and has a striated digital pad and a well-developed hallucal pad marked with a long and conspicuous striated area, which may or may not be confluent with a longer but similar striated area on the metatarsal pad behind it. Similar long and conspicuous striated areas are present upon the external metatarsal pad and upon the three well-defined elements of the plantar pad. In the specimen of this species examined in a fresh state it was noticeable that the 2nd and 5th digits were a little thicker than the 3rd and 4th. (Text-fig. 37, B, p. 1058.)

*D. hallucatus* has a hind foot * like that of *D. maculatus*; but it is shorter and broader and has usually rather longer, more conspicuous striated areas on the pads. The digital pads, for example, are entirely covered with striæ, the area not being restricted to their tips The metatarsal pads are individually variable in length, the inner being sometimes confluent with the hallucal pad, sometimes separated from it. (Text-fig. 38, D, E, p. 1059.)

Of *D. albopunctatus* I have only seen dried skins; but the hind foot, as is known, resembles that of *D. maculatus* and *hallucatus* in possessing striated areas, although the striæ are less conspicuous and sometimes only visible in certain lights.

The hind foot of the other genera may be briefly dismissed.

In *Dasyuroides* † the foot is long, the hallux and metatarsal pads are suppressed, and the hairs invade the metatarsal area on both sides, reducing the naked squamous area even more so than in *Thylacinus*; and each of the three well-defined, but confluent, elements of the plantar pad has a large, conspicuous, elongated, smooth area representing the much smaller areas observable sometimes, at all events, in *Dasyurus geoffroyi* and *D. viverrinus* and the elongated striated areas of *D. maculatus* and *D. hallucatus*.

In *Dasycerus* (*Chætocercus*) *cristicauda* ‡ the foot is shorter than in *Dasyuroides* and retains the hallux, which is set some distance from the plantar pad, as in *Dasyurus geoffroyi*, and, as in that species, the hallucal pad is absent and the metatarsal pads are scarcely traceable on the sole, which is as naked as in *D. geoffroyi*. The three well-defined elements of the plantar pad have smallish oval central areas as in *Dasyuroides*, but these are striated as in *Dasyurus hallucatus*.

In *Phascogale*, with its numerous species, the hind foot § varies

* Figured by Bensley.

† Figured by Bensley and Boas (Biol. Meddel. (1), 8, 1918).

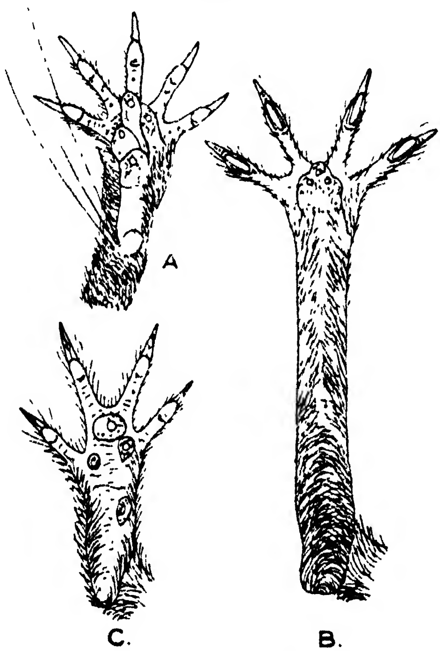
‡ Figured by Bensley and Wood-Jones.

§ The feet of *Ph. wallacei* and *penicillata* were figured by Thomas; of *P. flavipes* by Wood-Jones. The foot figured by Boas as that of a *Phascogale* has no trace of hallucal or metatarsal pads, and the three lobes of the plantar pad are provided with small, smooth, circular areas, thus differing from the foot of the species of *Phascogale*, as now understood. Possibly it represents the foot of *Dasycercus cristicauda*, which was formerly assigned to *Phascogale*.

in the length of the sole and of the digits and in the development of the pads; but except that the three elements of the plantar pad are more distinctly separated, a primitive character, I can find no other definable difference between the foot of this genus as now admitted and that of *Dasyurus hallucatus*. (Text-fig. 38, F, p. 1059.)

In *Sminthopsis* the foot* is also variable in length and pad

Text-figure 39.




A. Right fore foot of *Antechinomys spenceri*.
B. Right hind foot of the same.
C. The same of *Myrmecobius*.

development; but it apparently differs from that of *Phascogale* in the suppression of the metatarsal pads. The hallucal pad may be retained (*leucopus*, *murina*) or lost (*crassicaudata*). The foot is also longer and thinner than in *Phascogale*, and the metatarsus in some cases is more or less covered with hair.

In *Antechinomys* the hind foot † is remarkable for the extreme

* That of *S. leucopus*, *murina*, and *crassicaudata*, was figured by Thomas, and of *crassicaudata* by Wood-Jones.
† Figured by Thomas, Boas, and Wood-Jones.

elongation of the metatarsal area, which is also overgrown with convergent streams of hairs down to the plantar pad; for the confluence of the three elements of the plantar pad to form a single small heart-shaped pad, which however retains, at all events sometimes, three, small, smooth, circular areas; and for the compression of the digital pads. The digits, however, are evenly spaced and have exactly the same symmetrical arrangement as in *Thylacinus*, *Dasyurus*, and the other genera previously discussed. (Text-fig. 39, B, p. 1061.)

The modifications are of the hind foot in *Antechinomys* foreshadowed in a measure in *Sminthopsis*; but a glance at the figures will show that the foot differs more from the foot of e. g. *Dasyurus viverrinus* than does the hind foot of *Thylacinus*. So far, indeed, as the hind foot is concerned, there is nothing to warrant the dissociation of *Thylacinus* from the Dasyuridæ.

The hind foot of *Myrmecobius* * differs in some important respects from that of the Polyprotodonts hitherto noticed. Digits 2 to 5 are not arranged symmetrically in an evenly curved line outside the distal margin of the plantar pad. Digit 2 is set a little higher up the foot and farther away from digit 3, which is paired with digit 4; and digit 5 is still farther up the foot than digit 2 and farther from digit 4 than digit 2 is from digit 3. Digit 1, the hallux, is suppressed. The pads also are different. The median interdigital is enlarged and separated from the lateral interdigitals. The internal lateral interdigital is, however, close to it, while the external, the smallest of the three, is more remote. They are irregularly rounded, and each carries a small smooth central area. The metatarsal area is not granulated, but smooth, naked, and wrinkled, and on its inner side it carries an oval pad, similar to the three separated elements of the plantar pad. This is probably, I think, the inner metatarsal pad, and not the retained hallucal element of the plantar pad. (Text-fig. 39, C, p. 1061.)

Thus in the arrangement of the digits and the disposition of its pads the foot of *Myrmecobius* differs from that of all the other Australian Polyprotodonts.

There remain to be noticed some points connected with the retention or suppression of the hallux in the Australian Polyprotodonts. When retained it is always small and clawless, and can be of little service in grasping. Its size suggests the derivation of *Phascogale*, admittedly a primitive type of this group of Marsupials, from some mainly terrestrial stock of Didelphyidæ, like *Peramys*, and not from a scansorial stock like *Didelphys*, in which the hallux is large and powerful. In that case the arboreal species of Dasyuridæ have secondarily acquired that mode of life.

In most cases the retention of the hallux is associated with

* Figured by Thomas, Beas, and Wood-Jones.

the presence of conspicuously-striated, elongated areas on the metatarsal, carpal, and plantar pads, and with the retention also of the hallucal pad, which has a similar area. It is generally admitted that the Dasyuridæ with feet of this type are more arboreal on the whole than those with the central areas feebly striated or unstriated and reduced in size or absent.

In the more terrestrial or wholly terrestrial species the modifications of the foot take the direction of (1) suppression of the striæ, leaving the area smooth; (2) suppression of the area itself; (3) reduction or suppression of the metatarsal pads; (4) extension of the hair from the sides to cover, partly or rarely wholly, the metatarsal area; (5) suppression of the hallucal pad; (6) shifting of the hallux up the foot away from the plantar pad; (7) suppression of the hallux; (8) fusion of the three lobes of the plantar pad. The hind foot which exhibits these modifications in the highest degree is that of *Antechinomys*.

## The Pouch.

### (a) *The Pouch in the Males.*

The presence of a pouch, lodging the scrotum, in *Thylacinus* was recorded by Owen and subsequently by Beddard *, who observed it in a young specimen that died in the Gardens. It was well developed also in the adult male that died in Sept. 1914; and since the figure published by Beddard is difficult to reconcile with his description, which is accurate, a new figure and description may be useful. (Text-fig. 40, p. 1064.)

The integumental area from which the scrotum was suspended was naked, and insunk to form a tolerably deep cup-like depression defined anteriorly and laterally by a flap of skin higher in front than at the sides and gradually vanishing behind towards the middle line, so that the pouch was incomplete posteriorly and might be described as opening downwards and backwards. The tips of the hairs all round the pouch were directed towards it, those in front pointing backwards, those at the sides inwards, and those behind forwards. In the figure published by Beddard all the hairs point in the same direction, and the base of the tail, or what appears to have been intended for the base of the tail, is drawn above the broader end of the pouch, which, according to Beddard's description, is its anterior portion. The tail and the hair, indeed, in this figure appear to have been added to it from the artist's imagination, and not copied from the actual specimen.

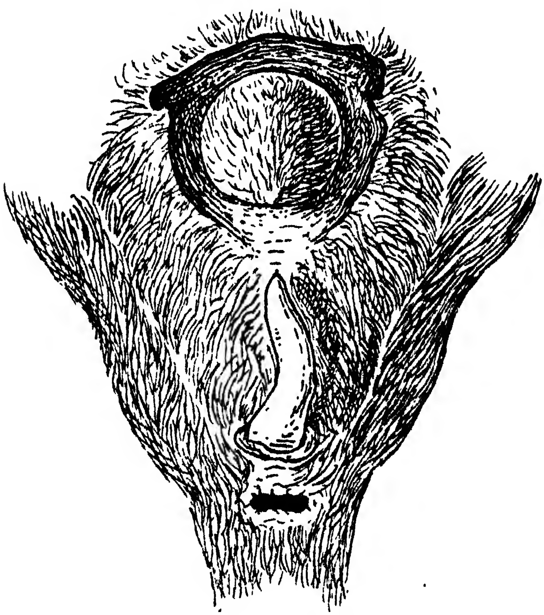
Males of other genera of Australian Polyprotodonts exhibit a similar naked area round the attachment of the scrotum, but in no case that came under my notice was this area sufficiently depressed to be describable as a pouch; and from the observations of others

* Proc. Zool. Soc. 1891, pp. 138–140, text-fig. 1. This paper also contains references to previous records of the discovery of rudimentary pouches in the males of Marsupials.

it appears that the scrotal pouch in this sex is better developed in fœtal or young individuals than in older specimens.

*Thylacinus* thus seems to differ from the other genera of Polyprotodont Marsupials in retaining a well-developed scrotal pouch throughout life. It is also the only polyprotodont which is digitigrade; and the two phenomena are, in my opinion, associated. The digitigrade feet have been acquired for the purpose of speed; and the function of the scrotal pouch is to prevent the violent swinging of the scrotum which would take place if there was no restraint upon its movement when the Thylacine was

Text-figure 40.



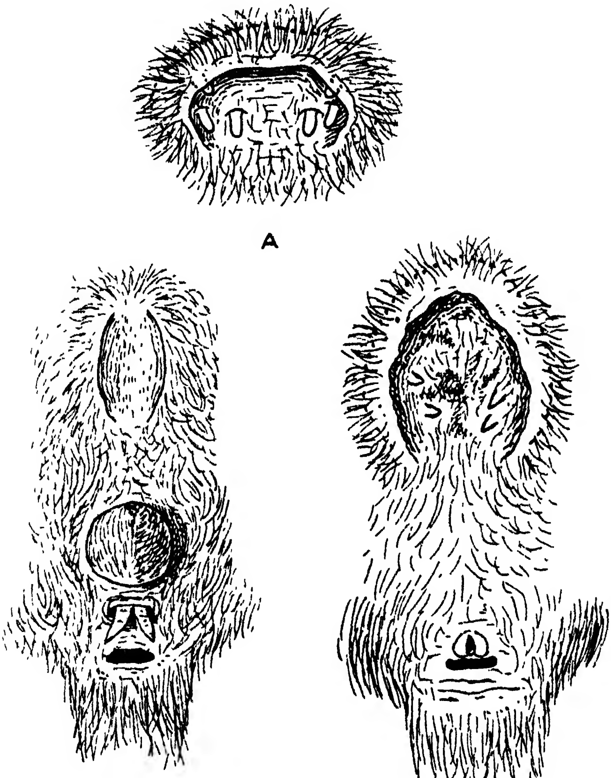
Anal and genital area of male *Thylacinus* showing the scrotal pouch and the extended penis.

in swift pursuit of its prey. That injury to the testes might result from this swinging is suggested by the length and slenderness of the stalk-like proximal portion of the scrotum by which the globular, testicular distal portion is suspended from the abdomen.

Although in *Thylacinus* the scrotal pouch both in structure and position recalls the mammary pouch of the female, it is doubtful, in my opinion, if the two can be regarded as homologous structures, as some authors hold. For in a male Azara's Opossum (*Didelphys marsupialis azaræ*) which died in

the Gardens in July 1914, I found a tolerably well-developed pouch in the middle of the lower surface of the abdomen, considerably in advance of the scrotum, entirely dissociated from it and occupying the same position as the mammary pouch

Text-figure 41.




A. Pouch of *Dasyurus maculatus* without young.

B. The same of *Sarcophilus*.

C. Anal and genital area of abnormal male *Didelphys marsupialis azaræ*, showing glandular pouch in front of scrotum.

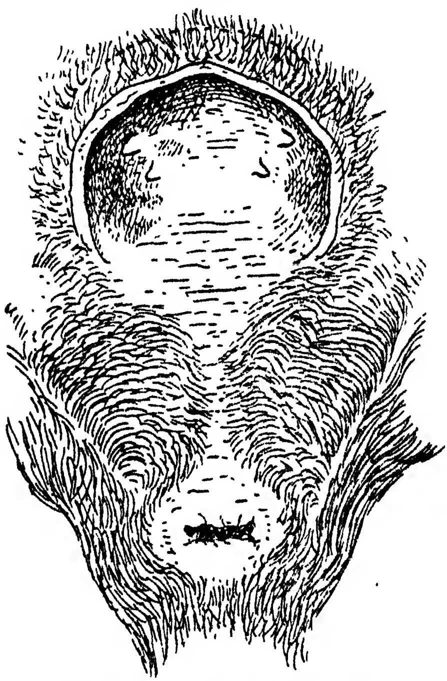
of the female of this species. This pouch was composed of two lightly-curved longitudinal flaps of skin separated in front and behind and forming the lateral borders of an ellipitical area scantily clothed with short yellow hairs, which, like the hairs all round the flaps, were covered with brown waxy secretion. The

condition observed suggested that this pouch was an active glandular scent organ, functionally similar to the median pectoral gland of *Myrmecobius* and *Petaurus breviceps*. The possibility that such a glandular structure was the origin of the marsupium is perhaps worth bearing in mind (text-fig. 41, C, p. 1065).

(b) *The Pouch in the Females.*

The pouch of the female Thylacine was described by Owen as opening backwards and possessing four mammæ. The adult

Text-figure 42.



Pouch and mammary area of *Thylacinus*.

female I examined agreed with the one seen by Owen. The pouch consisted of a nearly circular * area of naked skin bordered in front and at the sides with a rather shallow upstanding flap of skin with a strongly crescentic curvature. The flap became gradually shallower posteriorly on each side, ultimately blending with the abdominal integument, the points of origin being tolerably

* It must be remembered, however, that the shape of the pouch varies in this and other Marsupials in accordance with the stretching of the integument laterally or antero-posteriorly.

widely separated in the middle line. The four mammæ were symmetrically arranged in pairs, the two on each side being tolerably close together but widely separated from the corresponding mammæ of the opposite side, the anterior being farther apart than the posterior. The hairs on the abdomen surrounding the pouch were directed towards it, as in the case of the male; and between the pouch and the cloacal orifice the points of the hairs were directed inwards towards the middle line, leaving a narrow strip of naked skin forming an ill-defined passage between that orifice and the mammary area (text-fig. 42, p. 1066).

In *Sarcophilus*, as in *Thylacinus*, the mammary area is surrounded in front and laterally by a crescentic or horseshoe-shaped flap of skin; but this flap is relatively deeper and approximately the same depth at the sides and in front except at the posterior end, where it fades away into the abdominal integument. The space circumscribed by the flap is hairy, and in the two examples examined there were two pairs of mammæ as in *Thylacinus* (text-fig. 41, B, p. 1065).

A similar pouch was observed in an adult female of *Dasyurus maculatus*; but in this animal there were three pairs of mammæ arranged in two rows obliquely converging towards the posterior entrance to the pouch.

Thus in these three species a well-developed, or moderately well-developed, pouch, defective posteriorly and with its orifice opening downwards and backwards, is present when there are no young to make use of it. It is not acquired at the period of lactation: and, so far as I am aware, there are no observations suggesting that it becomes enlarged at that period.

In *Dasyurus viverrinus*, however, the pouch, as observed by others, is, or at all events may be, developed periodically to accommodate the young. In one specimen of this species examined in the Prosectorium there was no trace of the pouch, the mammary area consisting of an elliptical tract covered with short hairs and carrying three pairs of conical teats, set in two longitudinal rows, the whole being surrounded by a fringe of long rust-coloured hairs. But in an example in the British Museum the pouch containing young is well developed and of nearly equal depth all round, and formed by a circular flap of skin overgrown with long hairs overlapping the orifice, which opens directly downwards (text-fig. 43, D, E, p. 1068).

A pouch very similar to the last-described was present in an adult female of *D. geoffroyi*, but in this animal there were no young in the pouch; and since the conical shape of the teats did not suggest * that young had been removed from it, it appears that in *D. geoffroyi* as in *D. maculatus*, *Sarcophilus*, and *Thylacinus* the pouch is permanently retained. (Text-fig. 43, C, p. 1068.)

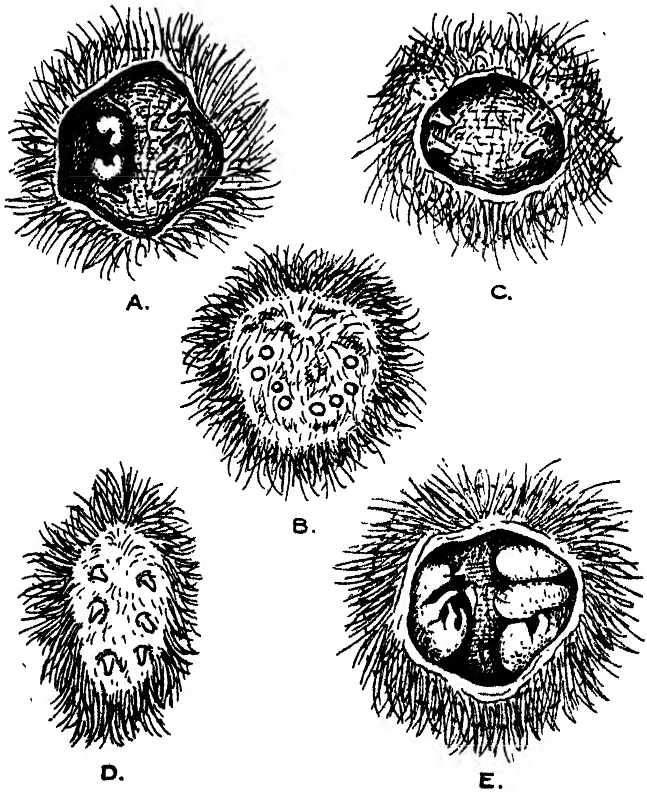
In a specimen of *D. hallucatus*, with newly-born young, the

* The teats of these marsupials are broad at the base and pointed apically when not in use; but during lactation they are slender and elongated, with a slightly expanded tip to fit into the mouth of the young and give it a secure hold.

pouch was circular as in *D. viverrinus* and *geoffroyi*, but shallower behind than in front and in an example without young, there was no trace of a pouch. (Text-fig. 43, A, B.)

It may be noted that in *D. maculatus* the pouch differs from

Text-figure 43.




A. Pouch of *Dasyurus hallucatus* with two young.
B. Mammary area of the same without young.
C. Pouch of *D. geoffroyi* without young.
D. Mammary area of *D. viverrinus* without young.
E. Pouch of the same with young.

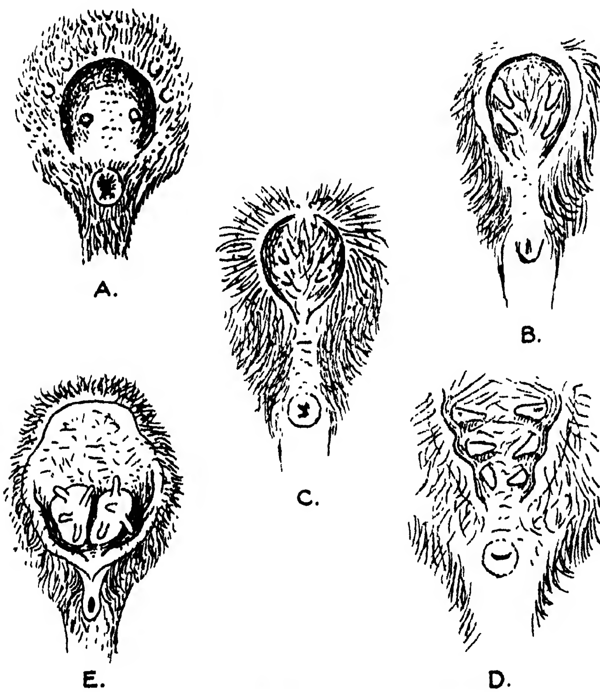
that of *D. virerrinus*, *geoffroyi*, and *hallucatus* in being defective and widely open behind.

In *Dasyuroides byrnei*, according to Baldwin Spencer *, the pouch, carrying six teats, is very slightly developed with two low

* Report of the Horn Exped. to Central Australia. Mammalia, p. 37.

lateral folds. In an example of this species in the British Museum the oval mammary area is scantily hairy and surrounded by long hairs, but shows no definite trace of marginal flaps of skin. The six teats are large and conical and arranged in two slightly converging longitudinal rows. The entire mammary area resembles tolerably closely that of the example of *Dasyurus*

Text-figure 44.



A. Pouch and mammary area of *Phascogale minutissima*.
B. The same of *Ph. dorsalis*.
C. The same of *Ph. lorentzi*.
D. The same of *Ph. thorbeckiana*.
E. The same of *Ph. flavipes*.

*viverrinus* without a pouch, described above. (Text-fig. 45, B, p. 1072.)

In *Dasycercus cristicauda*, according to Baldwin Spencer (*op. cit.* p. 22), the pouch, in which the teats may be 4, 6, or 8 in number, opens vertically downwards and has moderately developed lateral folds. Although Baldwin Spencer had females with and without young, he did not describe any variation in the

development of the pouch; but, according to Wood-Jones, the pouch in the quiescent state is practically obsolete; and this statement is borne out by an adult female in the British Museum, in which the tolerably elliptical mammary area, carrying six teats in two slightly convergent rows and depressed in two grooves, is not defined by marginal ridges of skin, but merely by the longer hairs of the abdominal surface. The area is continued back to the cloacal aperture by a naked strip of skin. (Text-fig. 45, C, p. 1072.)

In *Phascogale*, as is well known, the pouch is variable. In descriptive works it is usually dismissed as rudimentary, or obsolete, and at most represented by low folds of skin. There are, however, some interesting points connected with it.

As Thomas pointed out, it attains its greatest development in *P. minutissima*, one of the smallest representatives of the genus. In this species, indeed, it is relatively large and very similar to the pouch of *Sarcophilus* or *Thylacinus*, consisting of a crescentically-curved flap of skin, almost encircling the wide and long mammary area. It is deep in front, and becomes gradually shallower laterally and posteriorly and is defective in the middle line behind. It is relatively larger than in *Sarcophilus* and *Thylacinus*, and further differs in being set farther back so that the passage into it from behind is close to the cloacal orifice. Since this is the condition observed in a specimen without young, it seems that the pouch is a permanent feature in this species. In this specimen there are seven teats, four on one side, three on the other, the series being arranged in an irregular transverse ellipse (text-fig. 44, A, p. 1069).

In *P. lorentzi* the pouch is nearly as well developed as in *P. minutissima*, and tolerably similar to it except that it is smaller in the middle line than at the sides in front, less defective behind and more forward in position, the passage to it being farther from the cloacal aperture, with which it is connected by a longish narrow tract of naked skin. The example of this species examined was without young, and the teats were four in number (text-fig. 44, C, p. 1069).

A very similar pouch is present in an example of *P. dorsalis* without young and with only two pairs of large teats arranged as in *Sarcophilus* and *Thylacinus*. In this species also there is a smooth tract of skin passing from the cloacal aperture forwards to the posterior passage to the pouch. (Text-fig. 44, B, p. 1069.)

In a female of *P. thorbeckiana*, without young and with three pairs of large teats arranged in two posteriorly convergent rows, the pouch is represented by two thick lateral ridges of skin, each as long as and close to the adjacent line of teats. Thus the mammary area, which is thickly hairy, is widely open in front and narrowly open behind, and the posterior passage to it, which is tolerably close to the cloacal aperture, is connected therewith by a naked tract of skin. (Text-fig. 44, D, p. 1069.)

In a specimen of *P. swainsoni*, without young, the mammary area forms a wide heart-shaped scantily hairy tract entirely surrounded by a very slightly raised ridge of skin but sharply defined by the longer abdominal hairs round it. There are five teats on its right side and four on the left, somewhat irregularly arranged, but forming two lightly-curved posteriorly convergent series. (Text-fig. 45, A, p. 1072.)

In two specimens of *P. flavipes*, with young, the mammary area is a large conspicuous tract of nearly naked skin, but there is no definite pouch, the edges of the area being merely slightly raised. There are eight teats irregularly arranged, but they present the peculiarity of being raised upon a pair of irregularly oval eminences separated in the middle line and set on the posterior half of the mammary area, which extends backwards almost as far as the cloacal orifice. (Text-fig. 44, E, p. 1069.)

Finally, in five specimens of *P. unicolor* the whole abdominal region is uniformly covered with hairs, there being no mammary area defined by the character of its hairs and no trace of a pouch. The mammary area appears to be indicated by a small patch lying close to the cloacal orifice and marked by glandular secretion adhering to the base of the hairs that cover it.

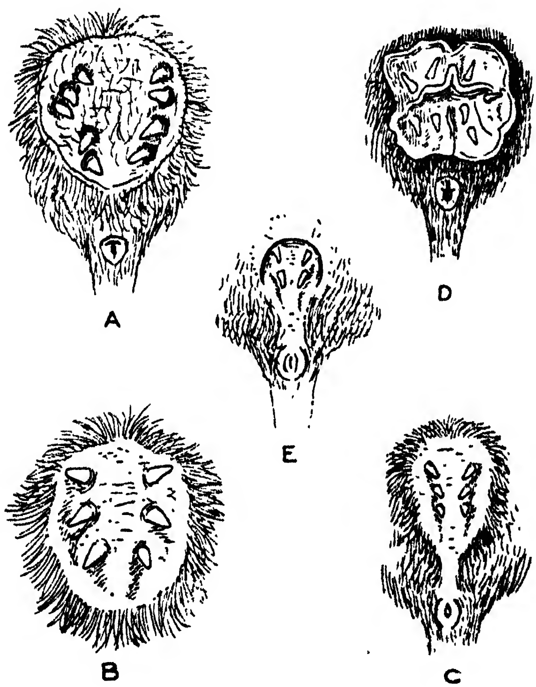
In this genus, therefore, there is extreme variation in the development of the mammary area, of the teats, and of the pouch, some species like *P. minutissima* having the pouch as well developed and the mammary area as well defined as in any Polyprotodont Marsupial; whereas in *P. unicolor* there is no trace of a pouch or of differentiated mammary area, the abdomen being uniformly covered like that of an ordinary placental mammal.

In *Sminthopsis*, according to Thomas, the pouch is well developed. This statement was confirmed by Wood-Jones in connection with *S. murina* and *crassicaudata*.

A female of *S. crassicaudata* in the British Museum has a very remarkable pouch, unlike that of any Marsupial I have seen. The raised edges of the mammary area, instead of inclining inwards over the area, diverge all round it, so that the flaps form an area wider at its free edge than along its line of attachment to the abdomen. This pouch, therefore, is not insunk, but stands away from the abdomen and may be described as saucer-like. The edge, however, is broadly lobate and foliate, the whole structure recalling superfically the expanded petals of a flower. Moreover, the anterior portion of the pouch is separated from the larger posterior portion by a low irregularly-curved ridge of skin which in the middle line forms a forwardly-directed angular loop which, with a notch in the anterior edge of the pouch, divides the anterior compartment into a right and left portion. The posterior compartment is also partially divided by a lower, thinner, median sinuous longitudinal ridge. There are eight

teats asymmetrically arranged. Two on the right side are set in front of the transverse ridge and two behind it, whereas on the left there is one in front of it, one just behind its outer end, and two in an obliquely longitudinal line. The pouch is no doubt partitioned for the accommodation of the young. It would be of interest to ascertain if the pouch of *S. murina* is similar to that of *S. crassicaudata*. (Text-fig. 45, D.)

Text-figure 45.




A. Mammary area of *Phascogale swainsoni*.
B. The same of *Dasyuroides byrnei*.
C. The same of *Dasycercus cristicauda*.
D. Pouch of *Sminthopsis crassicaudata*.
E. The same of *Antechinomys spenceri*.

*Antechinomys* is usually stated to have no pouch. Baldwin Spencer confirms Krefft's assertion of its absence in *A. laniger*, saying there is no trace of a pouch, no folds of any kind being distinguishable, and the whole mammary area is thickly covered with hair. Of *A. spenceri*, Wood-Jones says the pouch is entirely absent and that the nipples, six in number, are arranged in a circle. But in an example of this species in

the British Museum the pouch, which carries no young, is well developed and consists of a crescentic flap of skin encircling the mammary area in front and laterally, its narrowed posterior ends being tolerably far apart so that there is a wide passage into it, lying some distance in advance of the cloacal orifice. This pouch is very like that of *Sarcophilus* or *Thylacinus*; and it is interesting to note that this little Marsupial, which hops like a Kangaroo, has not acquired the forwardly-opening pouch as in that animal, but retains the primitive backwardly-opening pouch characteristic of the cursorial polyprotodonts. The teats in this specimen are six in number, arranged symmetrically in pairs and forming two posteriorly convergent straight lines. (Text-fig. 45, E, p. 1072.)

### Old and New Views of the Affinities of *Thylacinus* and *Myrmecobius*.

Judging from modern text-books and memoirs, two considerably divergent views regarding the systematic position of *Thylacinus* are prevalent. For the old view adopted by most European writers, it is needless to go farther back than Thomas's Catalogue of the Marsupials, 1888. In this the Polyprotodont Marsupials are classified as follows:—

**Polyprotodontia.**

Fam. Peramelidæ (*Peragale*, *Perameles*, *Chœropus*).

Fam. Dasyuridæ.

Subfam. Dasyurinæ (*Thylacinus*, *Sarcophilus*, *Dasyurus*, *Phascogale*, etc.).

Subfam. Myrmecobiinæ (*Myrmecobius*).

Fam. Didelphyidæ (*Didelphys*, *Chironectes*).

The subsequent addition of a few genera, including *Notoryctes*, the representative of another family, does not affect the question at issue. This classification clearly expresses the opinion that *Thylacinus* is essentially one with the rest of the Australian Dasyurines, the differences between it and *Sarcophilus* being equivalent, or approximately equivalent, to the differences between *Sarcophilus* and *Dasyurus*, or *Dasyurus* and *Phascogale*. The classification also indicates that *Thylacinus* is much more nearly akin to *Dasyurus*, *Phascogale*, *Antechinomys*, and the rest than is *Myrmecobius*.

The other view is of later date, and was apparently promulgated in 1903 by Bensley *, who in his phylogenetic table of this group of Australian Polyprotodonts derives *Sarcophilus*, *Dasyurus*, *Antechinomys*, *Sminthopsis*, etc., from *Phascogale*, or a *Phascogale*-like form, *Myrmecobius* being a branch of the same tree. *Thylacinus*, on the contrary, is marked interrogatively only as

* Trans. Linn. Soc., Zool. (2), ix. pt. iii. pp. 83–214 (1903).

*possibly and independently descended* from the same *Phascogale*-like ancestor, such resemblances as it exhibits to *Sarcophilus* and *Dasyurus* being due, it is said, to convergent adaptation (*op. cit.* p. 193). On this subject he remarks (*op. cit.* p. 194): "*Thylacinus*, so far as may be judged from dentition and foot structure, may be a derivative of *Phascogale*" and "*Sarcophilus* has no relation with the remaining specialized carnivorous form, *Thylacinus*. . . . *Thylacinus* is a foreign element in the Australian series." Also on p. 205 he wrote: ". . . . there are no definite reasons for believing *Thylacinus* to have a special affinity with the Dasyuridæ." Finally, on p. 209, he said: "The dental resemblances of *Thylacinus* to the Sparassodonts are sufficiently close to warrant a belief in their common origin. Even so, however, there is no evidence that the evolution of *Thylacinus* has been connected in any way with that of the Dasyuridæ, the reverse being indicated by the fact that the various forms of the Dasyuridæ present successive stages of a dental evolution which, while carnivorous in its character as in *Thylacinus*, is otherwise of a totally different facies."

This opinion of Bensley's was adopted by Gregory * and by Osborn † in 1910, whose classification of the typical Polyprotodont Marsupials was for all practical purposes the same. I quote Osborn's, which, in comparison with Thomas's, set forth above (p. 1073), clearly indicates the divergence of view as regards the status of *Thylacinus*:—

**Didelphoidea.**

Fam. DIDELPHIIDÆ.

Fam. MYRMECOBIIDÆ.

Fam. DASYURIDÆ.

Subfam. PHASCOGALINÆ (*Phascogale*, *Antechinomys*).

Subfam. DASYURINÆ (*Dasyurus*, *Sarcophilus*).

Fam. THYLACINIDÆ.

Subfam. THYLACININÆ (*Thylacinus*).

Subfam. BORHYÆNINÆ (Sparassodonts of the Eocene and Miocene of S. America).

Scott ‡ also in 1913 accepted the view that *Thylacinus* is a Sparassodont, a conclusion involving the seductive hypothesis of a migration of Marsupials from South America to Australia by a South Pacific land-bridge.

The influence of Bensley's views is also apparent, I think, in the two most recent classifications of the Polyprotodonts, namely those published by Wood-Jones § and Cabrera ‖, in which *Thylacinus* is severed from the Dasyuridæ as the type

* Bull. Amer. Mus. Nat. Hist. xxxvii. (1910).
† 'The Age of Mammals,' p. 517 (1910).
‡ 'A History of the Land Mammals of the Western Hemisphere,' p. 635.
§ 'The Mammals of South Australia, Pt. I.,' p. 84 (1923).
‖ 'Genera Mammalium: Monotremata and Marsupialia,' pp. 70–71 (1919).

of a special family, Thylacinidæ; and since the same rank is given to *Myrmecobius*, it may be inferred that, in the opinion of these authors, *Thylacinus* differs approximately as much from the Dasyuridæ as does *Myrmecobius*.

### The Systematic Position of *Thylacinus* and *Myrmecobius* attested by External Characters.

It may be interesting to revise in detail the organs described in this paper to see whether they support the older view, expressed in Thomas's classification, that *Thylacinus* is a specialized genus of the Dasyuroid stock, or the newer view, advocated by Bensley and those who follow him, that *Thylacinus* has had an independent origin from the Dasyuridæ, and resembles them merely in convergent adaptive characters or in characters inherited from a remote common ancestor.

(1) *The Facial Vibrissæ.*—So far as these tactile bristles are concerned, *Thylacinus* differs in no respect from the Dasyuridæ.

(2) *The Rhinarium.*—The rhinarium in *Thylacinus* is essentially as in the Dasyuridæ. The philtrum, it is true, differs from that of such genera as *Dasyurus* and *Sarcophilus* in being longer, narrower, and in the parallelism of its lateral grooves; but these differences are not greater than those that obtain in the philtrum within the limits of the species assigned to *Phascogale*; and the philtrum of *Antechinomys* differs as much from that of *Phascogale wallacei* as the philtrum of *Thylacinus* differs from that of *Dasyurus*.

(3) *The Ear.*—The ears in *Dasyurus*, *Sarcophilus*, *Phascogale*, *Antechinomys*, etc., are all constructed on the same plan, differing only in presenting minor modifications in structural details; and the ear of *Thylacinus* does not deviate in any particulars from that type.

(4) *The Feet.*—The feet of *Thylacinus* show close resemblances to those of the typical Dasyuridæ in the granulation of the pads and naked areas and the disposition of the digits. The modifications they present are adaptations to the digitigrade gait subservient to the chase. The claws are shorter and blunter, the plantar pads on the whole a little more cushion-like, and the pollex a little shorter. In the complete suppression of the tuft of carpal vibrissæ *Thylacinus* is admittedly unique; but analogy supplied by other mammals does not countenance the attachment of great systematic importance to this defect. On the whole I think it is surprising that the feet differ so little from those of *Sarcophilus*, for example; in fact, their general resemblance to those of that genus and others, despite their functional difference, is, to me, strong evidence of affinity. At all events it is abundantly clear that the

hind feet differ much less from those of *Sarcophilus*, for example, than do the hind feet of *Antechinomys*, in which the digitigrade gait for hopping reaches the extreme in this group of Marsupials.

(5) *The Pouch.*—The pouch of the female *Thylacinus* is structurally identical with that of *Sarcophilus* and some other genera and species. That of the male is, so far as I know, unique in its development and persistence. On the other hand, it is clearly nothing but a specialized development of the naked circumscrotal area seen in other genera of Dasyuridæ.

Judging then from the characters discussed in this paper, it appears to me obvious that we have complete evidence of tolerably close affinity between *Thylacinus* and the Dasyuridæ. To set these resemblances aside as of no importance is to deny the fundamental axiom of taxonomy that likenesses imply affinity.

The external characters of *Myrmecobius* remain for consideration :—

(1) *The Facial Vibrissæ.*—*Myrmecobius* differs from the Dasyuridæ and from *Thylacinus* in the reduction in number and length of the facial vibrissæ in accordance with its ant-eating habits. It is unique in the complete suppression of the interramal tuft.

(2) *The Rhinarium.*—In the single specimen available the rhinarium is somewhat distorted by crushing; but, so far as can be observed, it does not differ essentially from that of the Dasyuridæ.

(3) *The Ear.*—The ear differs from that of the Dasyuridæ and *Thylacinus* in being narrowed and pointed distally, and simpler in structure owing to the absence, probably by suppression, of the naked space below the ridge which runs backwards beneath the supratragus.

(4) *The Feet.*—The fore feet differ from those of the Dasyuridæ and *Thylacinus* in the uneven spacing of the digits, of which 2, 3, and 4 form a distal trio with the 3rd slightly shorter than the 2nd and 4th: also the two interdigital elements of these three digits are set upon an undivided cushion-like pad, there being no large plantar pad formed by the fusion of four pads. The hind foot also does not exhibit the symmetrical disposition and even spacing of its four digits so characteristic of this foot in the Dasyuridæ and *Thylacinus*. The 3rd and 4th digits form a distal pair, with the 2nd above the 3rd, and the 5th still farther above the 4th. The interdigital pad between the 4th and 5th is remote from the much larger pad between the 3rd and 4th, and the corresponding pad between the 2nd and 3rd merely touches the larger pad mentioned. Thus there is no three-lobed plantar pad as in the Dasyuridæ and *Thylacinus*.

(5) *The Pouch.*—The pouch, being absent in the female as in some species of Dasyuridæ, supplies no characters for consideration.

From this enumeration of characters, to which the slender extensile tongue might have been added, it seems clear that in the structure of the facial vibrissæ, of the ear, and of the feet, *Myrmecobius* differs considerably more from the Dasyuridæ than does *Thylacinus*.

### The Systematic Position of *Thylacinus* and *Myrmecobius* attested by Dentition.

In the structure of the teeth Bensley chiefly found support for his view regarding the isolation of *Thylacinus* from the Dasyuridæ. It appears to me, on the contrary, that these organs bear out the conclusion that *Thylacinus* is tolerably closely related to the genera of that family.

Perhaps the most important evidence bearing on this question was supplied by Tomes's researches on the microscopical structure of the enamel * in Marsupials and Creodonts. He found, in the first place, that the enamel of *Thylacinus* is essentially as in the Dasyuridæ. In the second place, of *Borhyæna*, the type of the subfamily Borhyæninæ of the family Thylacinidæ of Osborn's classification, he wrote :—"There is ample evidence to say that the enamel of *Borhyæna* is essentially of the Carnivorous type, and bears no more resemblance to that of the Marsupials than does that of other Creodonts, . . . which show a close resemblance in their enamel to their descendants, the recent Carnivora. . . . . The histological structure of the enamel does not bear out the general resemblance in macroscopic structure between the teeth of Polyprotodont Marsupials and of the Creodonts. . . . The absence [in the teeth of Creodonts] of the peculiar stamp of the Marsupial, the tubular enamel, would justify us in saying that they certainly do not stand near to any Marsupial." Nothing can be clearer than the inference to be drawn from these facts, which Tomes himself regarded as surprising and disappointing.

With regard to their macroscopic structure, I agree with Thomas that the teeth of *Thylacinus* can be reasonably interpreted as comparatively simple modifications of the plan characteristic of the Dasyuridæ. To illustrate this, I subjoin sketches of the second upper molar of the left side and of the third lower molar of the right side of *Dasyurus maculatus*, *Sarcophilus*, and *Thylacinus*, and to render the comparison clearer have similarly lettered the homologous lobes.

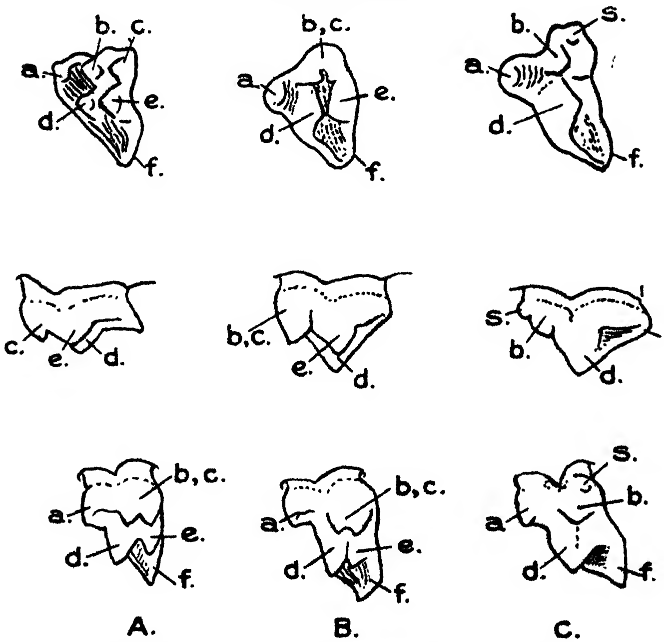
In *Dasyurus* the upper molar (text-fig. 46, A, p. 1078) is triangular, broad in front, with a prominent antero-external angle, a round lobate internal angle, and a longer, narrower, pointed posterior angle. The antero-internal angle carries a cusp (*a*), and externally to it the broad part of the tooth has four

* Proc. Zool. Soc. 1906, pp. 45–58. Tomes examined the teeth of a large number of Marsupials and Creodonts.

cusps arranged in pairs, making a quadrilateral, two in front (*b* and *c*) and two behind (*d* and *e*). They are well defined, but *d* is the largest. From *d* a cutting edge extends to the posterior angle, the surface of this region of the tooth being slightly hollowed.

In *Sarcophilus* this tooth is constructed on the same plan, but is more massive, the posterior angle is broader and blunter, and the antero-external angle larger and more lobate and carries the

Text-figure 46.




A. Second upper molar of left side of *Dasyurus maculatus*, seen from above, from the outer side and obliquely from the front.

B. The same of *Sarcophilus*.

C. The same of *Thylacinus*.

*a*, cusp of antero-internal angle; *b*, *c*, *d*, *e*, the four main cusps of the crown; *f*, the posterior angle; *s*, supernumerary cusp in C.

two cusps, *b* and *c*. These are set close together and are coalescent, so that the lobe that carries them may be described as apically bifid, the two cusps being separated by a narrow notch. Similarly the cusps *d* and *e* are closely juxtaposed and separated by a narrow notch, so that they suggest a single large apically bifid cusp. The cutting ridge running back from *d* is present, but the hollow on the posterior portion of the tooth is better defined. (Text-fig. 46, B.)

In *Thylacinus* the posterior part of the tooth is long and pointed as in *Dasyurus*, and the antero-external angle is large and lobate as in *Sarcophilus*; but the internal lobe is better defined than in either genus, being more constricted at the base. Cusp *b* of the anterior pair is large and functional; cusp *c* is absent; but there is a small supplementary cusp which is found in some species of *Phascogale*. Cusp *e*, which is reduced in *Sarcophilus*, is altogether suppressed, leaving cusp *d* to stand alone as the point of a cutting blade which is continued posteriorly by a sharp ridge running back to the posterior angle. The outer side of the hollow on this part of the tooth is sloped away so that its external margin is not so well defined as in *Sarcophilus*. (Text-fig. 46, C, p. 1078.)

This tooth, therefore, is essentially the same in structure as in *Sarcophilus* and *Dasyurus*, and differs mainly from that of *Dasyurus* in the complete suppression of cusps *c* and *e* and the enlargement of cusp *d*, the result being a cutting rather than a crushing tooth. But reduction of the two cusps in question is foreshadowed in *Sarcophilus*.

The lower molar in *Dasyurus* is narrowed in front and carries a single cusp, *a*. Behind this on the outer side is a very large, pointed cutting cusp, *b*, and behind *b* there is a smaller cusp, *c*. On the inner side of *b* there is a very distinct cusp, *d*, and on the inner side of *c* lies a fifth cusp, *e*, the posterior portion of the tooth carrying *c* and *e* being broad, with the margin convex and scarcely produced in the middle line. (Text-fig. 47, A, p. 1080.)

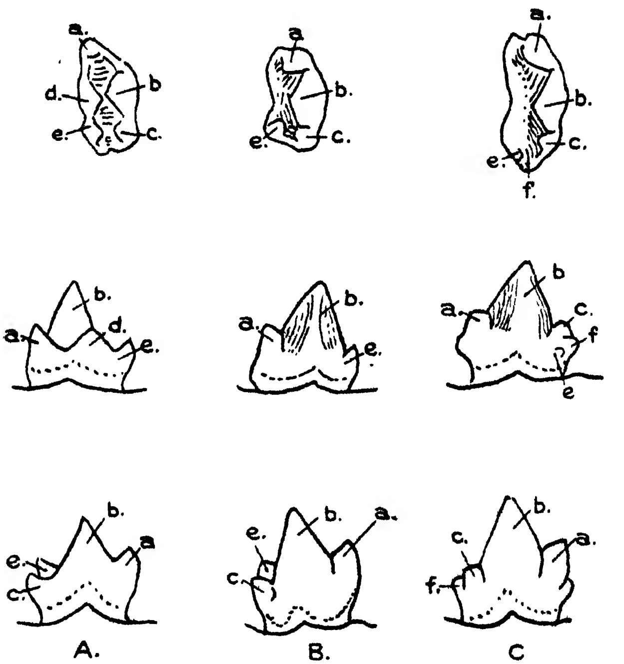
In *Sarcophilus* this tooth differs principally from that of *Dasyurus* in the total suppression of the median cusp, *d*, on the inner side. For the rest the whole tooth is stouter, being more rounded and not angularly produced in front, and the posterior portion, carrying cusps *c* and *e*, is broader, with the margin obliquely truncated and not at all produced in the middle line posteriorly. (Text-fig. 47, B, p. 1080.)

In *Thylacinus* this tooth resembles that of *Sarcophilus* in the complete suppression of cusp *d*, so that cusp *b*, as in *Sarcophilus*, acts as a piercing, cutting blade, without interference from the supplementary cusp *d*. The anterior part of the tooth carrying cusp *a* is broader than in *Dasyurus*, but not so broad as in *Sarcophilus*, and its edge is notched and it carries a very small supplementary cusp on its outer side in front on the root of cusp *a*. The posterior part of the tooth carrying cusps *c* and *e* is about as broad as in *Dasyurus*; but its posterior border projects a little in the middle line and carries a small median supplementary cusp, *f*. Moreover, cusps *c* and *e* are differently proportioned from what is seen in *Dasyurus* and *Sarcophilus*, the outer cusp *c* being much larger than the inner cusp *e*, and completely concealing it when the tooth is viewed from its outer aspect, the converse being the case in *Sarcophilus* and *Dasyurus*. (Text-fig. 47, C, p. 1080.)

In the number of the teeth *Dasyurus* and *Sarcophilus* are alike

and differ from *Thylacinus*, the formula of the cheek-teeth in the first two being *pm.* $\frac{2}{2}$, *m.* $\frac{4}{4}$, the 2nd and 4th premolars being suppressed, whereas in *Thylacinus* it is *pm.* $\frac{3}{3}$, *m.* $\frac{4}{4}$, only the 2nd premolar being suppressed. But in this respect *Thylacinus* resembles *Phascogale*; and since *pm.* 4 is a functional tooth in the

Text-figure 47.




**A.** Upper, inner, and outer surfaces of third lower molar of the right side of *Dasyurus maculatus*.

**B.** The same of *Sarcophilus*.

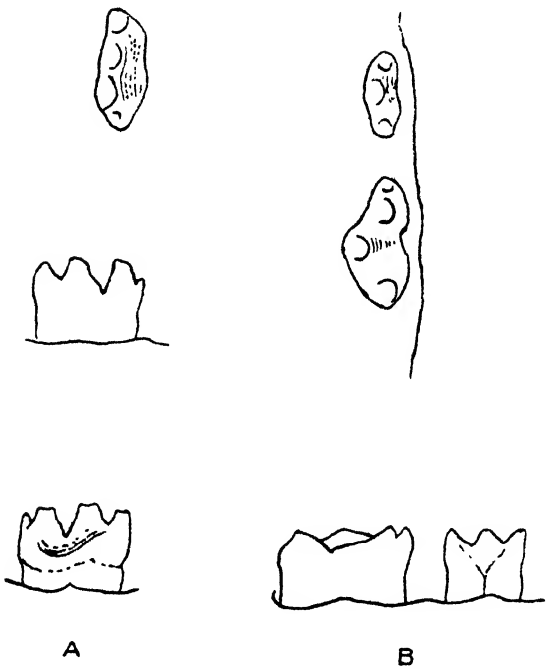
**C.** The same of *Thylacinus*.

*a*, anterior cusp; *b*, external main cusp; *c*, posterior external cusp; *d* (present only in A) internal median cusp; *e*, posterior internal cusp; *f* (present only in C) heel.

more primitive forms of the family, its retention in *Thylacinus*, with long, snapping jaws affording abundance of room for its presence, is not perhaps surprising. When, indeed, *Phascogale* and other genera akin to it showing the range in variation in the dentition of the Dasyuridæ are taken into consideration, the reasons for regarding *Thylacinus* as a descendant from a distinct stock of Marsupials appear to me to be of small account.

Of still smaller account do they become when *Myrmecobius* is held, as Bensley held it, to be an offshoot from the Dasyuridæ, for that view admits extreme plasticity in the teeth in that stock. In *Myrmecobius* all the cheek-teeth are variable in size and shape, are frequently not alike on the two sides, and the molars are excessively reduced in size and multiplied in number; and

Text-figure 48.



A. Upper, inner, and outer surfaces of third lower molar of *Myrmecobius*.
B. Upper and outer surfaces of third and fourth upper molars of the same.

the homologies between their cusps and those of the typical Dasyuridæ are too obscure to determine (text-fig. 48, A, B) *.

Hence it appears to me that the inclusion of *Myrmecobius* in the Dasyuroid stock and the exclusion of *Thylacinus* therefrom is an apt illustration of the simile, swallowing a camel and straining at a gnat; and this applies to the external characters

* Nevertheless, Bensley's tabular classification of *Thylacinus*, the typical Dasyurids, and *Myrmecobius* by their teeth makes it appear that *Myrmecobius* differs less in dentition from the Dasyurids than does *Thylacinus*. This tabulation was clearly arranged to fit the theory, not the facts.

discussed in this paper as well as to the teeth. In my opinion the evidence in the case of *Thylacinus* points to tolerably close kinship with the Dasyuridæ, whereas in the case of *Myrmecobius* the evidence points to comparative remote kinship with that family; and this view was expressed in Thomas's classification, in which *Thylacinus* was retained in the subfamily Dasyurinæ, and *Myrmecobius* separated as the type of the subfamily Myrmecobinæ. It is the fashion nowadays to give full family rank to *Myrmecobius*. That is a justifiable, if small, matter, because the genus presents several well-marked characters which are not found, or even foreshadowed, in any genera of Dasyurids, and are not easily explained by its formicivorous habits. *Thylacinus*, on the contrary, presents cross resemblances to more than one genus of Dasyurids, and its peculiarities are foreshadowed in those genera, and are, at least in some cases, to be explained by its adoption of cursorial predatory habits demanding comparatively slight structural changes.

## New Genera related to *Dasyurus*.

From the evidence supplied by the variations in the rhinarium, ears, marsupium, and other characters, it seems probable that *Phascogale* will prove to be divisible into several genera. Available names are *Phascogale*, *Antechinus*, and *Myoictis*, of which the typical species are respectively *penicillata*, *flavipes*, and *wallacei*, according to Thomas's selections in 1888. Of these, *Myoictis* has recently been resuscitated by Cabrera as a subgenus; but until more spirit-preserved material than is now available comes to hand for examination and comparison, it will be wiser to leave the genus in its present somewhat chaotic state.

*Dasyurus*, however, may, I think, be usefully subdivided to emphasise the marked peculiarities of some of its species. The type is *viverrinus*, and no other generic names seem to have been applied to this or other species. The genera into which I propose to divide the genus may be briefly diagnosed as follows *:—

### Dasyurus E. Geoff.

Type *viverrinus* Shaw.

Hallux suppressed; hallucal pad suppressed; lower sides of fore and hind feet uniformly granular, generally, at all events, without trace of central area on lobes of plantar, carpal, and metatarsal pads.

### Notoctonus, gen. nov.

Type *geoffroyi* Gould.

Related to *Dasyurus*, but retaining the hallux, which, however, emerges high up the metatarsal area; hallucal pad suppressed; feet uniformly granular, with at most a small, circular, smooth area on the lobes of plantar pads and of carpal pad.

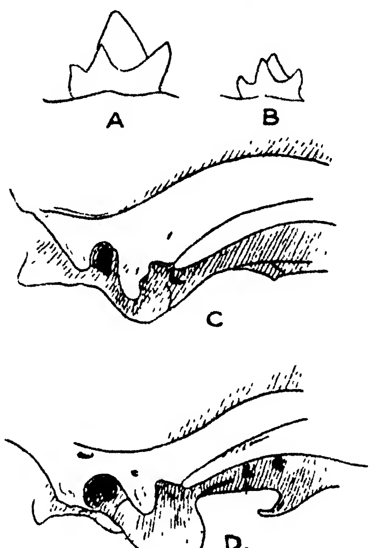
* Most of the characters here made use of may be found in Thomas's Catalogue.

SATANELLUS, gen. nov.

Type *hallucatus* Gould.

Resembles *Notoctonus* in the retention of the hallux, but differs in the retention also of the hallucal pad, the lower emergence of the hallux nearer the plantar pad, and the presence on the metatarsal, carpal, and plantar pads of well-defined, elongated, striated areas, the conspicuous striation of a large area of the digital pads and the paired scaling of the under side of the digits. (Text-fig. 38, D, E, p. 1059.)

Text-figure 49.




A. Third lower molar of *Dasyurus maculatus*.
B. The same of *D. hallucatus*.
C. Side view of auditory region of the skull of *D. maculatus*.
D. The same of *D. hallucatus* showing the inflated bulla.

STICTOPHONUS, gen. nov.

Type *maculatus* Kerr.

Feet like those of *Satanellus*, except for the restriction of the striated areas on the digital pads to a narrow distal band and the uniformly granular sculpturing of the lower sides of the digits (text-fig. 35, B, p. 1053). Differs also from *Dasyurus*, *Notoctonus*, and *Satanellus* in having much flatter and less globular auditory bullæ; in the large size of the main cusp of the lower molars, which is much higher than the internal median cusp, the latter being correspondingly reduced; and, so far as is known, in having the pouch in the female widely open behind (text-fig. 41, A, p. 1065).

The above-mentioned characters used for the severance of *Dasyurus* into four genera may be summarized as follows :—

*a.* Hallux suppressed ........................................................ *Dasyurus.*
*a'.* Hallux retained.
  *b.* Hallucal lobe of plantar pad suppressed and the hallux farther from plantar pad; metatarsal pads almost wholly suppressed, without central area; lobes of plantar pads at most with small, smooth circular areas .................... *Notoctonus.*
  *b'.* Hallucal lobe of plantar pad retained; hallux nearer the plantar pad; metatarsal pads with elongated striate areas; similar areas on the carpal pads and the lobes of the plantar pads.
    *c.* Lower side of digits uniformly granular; digital pads similarly granular, with comparatively small striate area. Auditory bulla low. Main cusp of lower molars much larger than median internal cusp, which is smaller than anterior cusp. .............................. *Stictophonus.*
    *c'.* Lower side of digits with paired scales; digital pads with much larger striate area. Auditory bulla high and globular. Main cusp of lower molars not much larger than internal cusp, the latter not smaller than anterior cusp ........................................................ *Satanellus.*

These genera show some interesting adaptive deviations. The most primitive and the most like *Phascogale* is *Satanellus hallucatus*. From this, *Stictophonus maculatus* departs on one side in the direction of being more predatory in habits and more carnivorous in diet, the trenchant teeth being associated, as in *Sarcophilus*, with reduction of the bulla. On the other side departs *Notoctonus geoffroyi* in the direction of being less scansorial in habits than *Satanellus hallucatus*, as indicated by the structure of the feet; and from *Notoctonus geoffroyi* may be derived *Dasyurus viverrinus*, which shows adaptation of the feet similar in a great measure to those of *Sarcophilus*.

# 54. The External Characters of the Patagonian Weasel (*Lyncodon patagonicus*). By R. I. Pocock, F.R.S., F.Z.S.

[Received June 14, 1926: Read November 16, 1926.]

(Text-figures 50–54.)

When my paper "On the External Characters and Classification of the Mustelidæ"* was published, I had not seen a freshly-preserved specimen of the rare South American Weasel *Lyncodon*, my observations upon the genus and the conclusion I reached as to the systematic value of its characters being based upon an examination of the dried skins and a few broken skulls preserved in the British Museum. Quite recently, however, an adult female preserved in alcohol was presented to the Museum by Col. Morley C. Knight, who procured it at Bonifacio in Buenos Ayres, and the following notes, amplifying and, in some cases, correcting my previous statements, have been drawn up from an examination of it.

## *The Head and its Organs.*

The shape of the head is like that of *Mustela*, the crown being long and low and the muzzle short and deep.

The *Facial Vibrissæ* are well developed, long, and slender. There are four or five superciliaries, the longest of which reaches back beyond the ear; some of the mystacials also reach beyond the ear, but the two genal tufts, occupying the normal position for the Mustelidæ, are not easy to detect, since each consists of two short slender vibrissæ which must be almost functionless. There is a row of submentals on each side of the lower jaw, and at least one of the interramals is long (text-fig. 50, C, p. 1086).

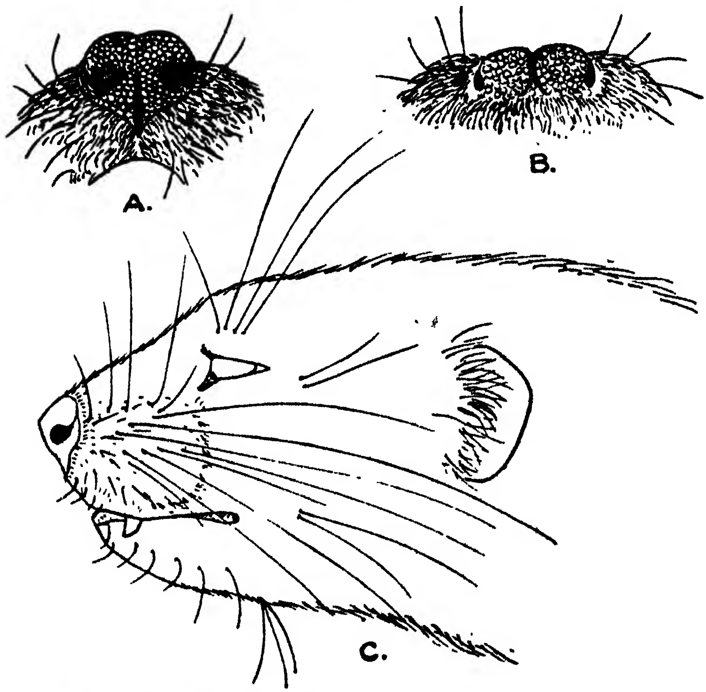
The *Rhinarium* is areolated; its upper surface is about twice as wide as long, the hairs on the muzzle extending forwards to the posterior angle of the nostrils, and it is mesially grooved. Seen from the front it is convex and mesially notched above and mesially grooved in its lower half. Its inferior and lateral margins up to the posterior angle of the nostrils are evenly convex, and there is a median inferior pointed projection representing an aborted philtrum. The upper lip is not cleft, the hairs merely showing an indistinct parting in the middle line (text-fig. 50, A, B, p. 1086).

The *Ear*, as could be seen on the dried skins, is greatly reduced and much smaller than in typical predatory Mustelidæ.

* Proc. Zool. Soc. 1921, pt. iv. pp. 803–837, 1921.

It is also simplified in structure; the supratragus, which is usually large and valvular in the family, is reduced to a soft indistinct ridge set high up in the cavity of the ear, and the anterior margin of the upper part of the cavity which normally projects backwards beneath the supratragus is merely represented by a soft and small flap of skin continuous with the margin above; the tragus, however, in a tolerably well-developed fleshy lobe, and the antitragus and intertragal notch are also defined. The

Text-figure 50.




A. Rhinarium of *Lyncodon* from before.

B. The same from above.

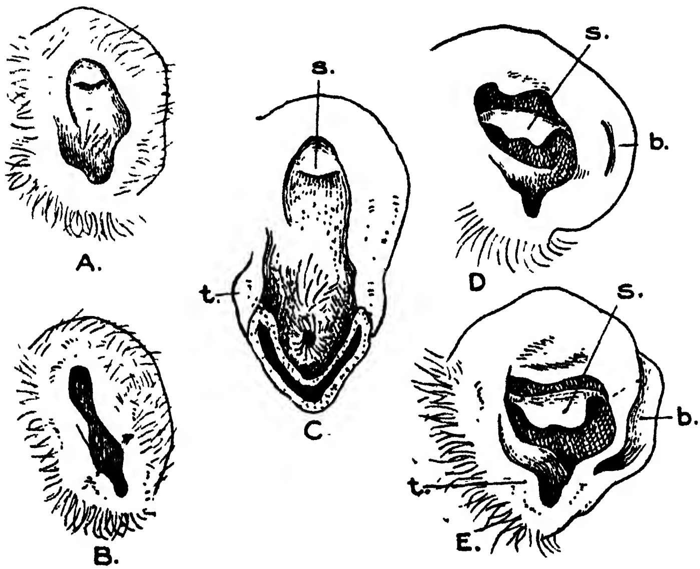
C. Side view of head of the same showing the vibrissæ and the small size of the ear.

lower portion of the cavity is hairy and the auditory orifice, which is set tolerably deep, is surrounded by a thickening of soft tissue covered with protecting hairs (text-fig. 51, A–C, p. 1087).

In the simplification of the ear *Lyncodon* differs markedly from *Mustela* and *Grison*. In both these genera the supratragus is large and valvular, and there is a small fleshy lobe above it, differentiated from the upper margin of the cavity. Also the anterior overfolded edge is continued backwards beneath

the supratragus to terminate in a thickening occupying the lower portion of the cavity above the auditory orifice. In *Mustela*, too, there is a very conspicuous marginal bursa. Even in *Grison* the bursa is retained as a shallow pocket, although it is noticeably degenerate as compared with that of *Mustela*. The ear of *Lyncodon*, indeed, is more like that of *Conepatus* and *Mephitis*. This likeness, however, must be regarded as purely adaptive. (Text-fig. 51, D, E.)

Text-figure 51.



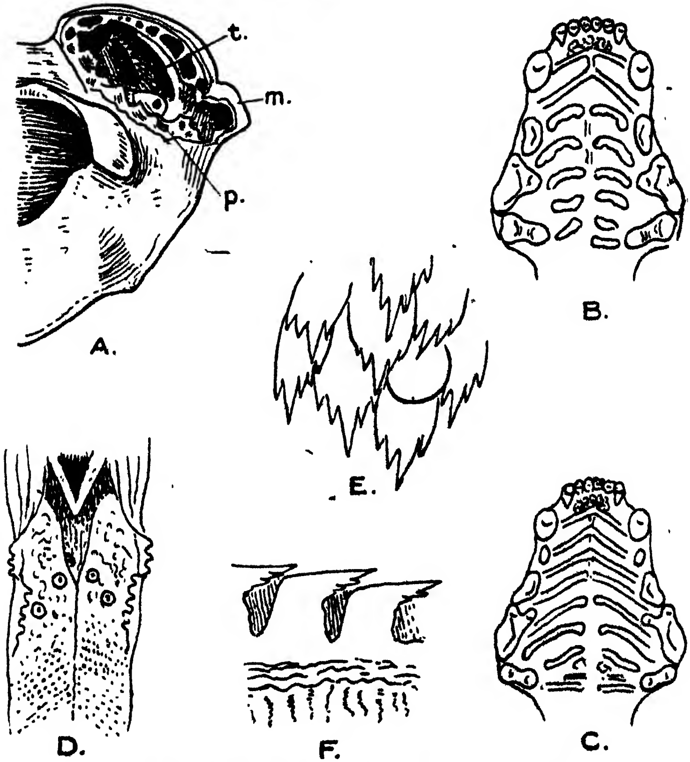

A. Ear of *Lyncodon* open.
B. The same partially closed.
C. The same on a larger scale open and with the lower portion cut through to show the auditory orifice.
D. The ear of *Grison*.
E. The ear of *Mustela erminea*.

*s*. supratragus, *t*. tragus, *b*. bursa.

*The Tongue and Mouth.*—The palatal ridges are well defined. The first forms a transverse arch between the canines, and between it and the incisor teeth there is a definite lobulated elevation. The second is obtusely angular, and runs forwards between the canines from a point on each side between the canines and the first retained premolar; the apex of its angle is connected with the middle of the first ridge by a short ill-defined longitudinal ridge. The 3rd, 4th, and 5th are slightly biconvex, with a median notch in front, dividing or almost dividing them

into two. The 3rd rises between the anterior ends of the first retained premolar ($pm^3$), and the 5th between the inner

Text-figure 52.




A. Posterior view of half the occipital region of *Lyncodon* with the left auditory bulla cut open to show the tympanic ring (*t*) in contact with the roof, the petrous portion (*p*) of the periotic, and the hollowed mastoid (*m*) with its cavity opening into the cavity of the bulla.

B. The palate of *Lyncodon*.

C. The palate of *Mustela erminea*.

D. Median and posterior portion of the tongue of *Lyncodon* showing principally the circumvallate papillæ and the lobulated fringe on each side of this area of the tongue.

E. Portion of the roughened surface of the tongue showing the tips of the denticulate papillæ and one rounded papilla.

F. Section showing the backwardly bent tips of three of the denticulated papillæ.

lobes of the carnassial ($pm^4$), the 4th occupying an intermediate position. The rest lying between the carnassials and the molars are short, mesially divided, and irregular in shape

and number, there being three on the left side and two on the right (text-fig. 52, B, p. 1088).

The palatal ridges in *Mustela erminea* and *putorius* are more complete and more numerous than in *Lyncodon*. The third and fourth are continuous across the middle line, and the fifth is only interrupted to a small extent. Behind the fifth they vary in the two European species. In an example of *M. erminea* the sixth is well developed, the seventh is as well defined and symmetrical as the third, fourth, or fifth of *Lyncodon*, and there are traces of three more behind it between the molars. In *M. putorius* the sixth may be broken up or tolerably well defined, and behind it there are asymmetrically-arranged fragments of three more. Thus nine or ten ridges are traceable in *Mustela* and seven or eight in *Lyncodon* (text-fig. 52, C, p. 1088). The palate of *Grison* is not available for comparison.

The tongue has a median groove which is tolerably widely dilatable proximally towards the epiglottis, shallow in the middle and deeper distally. Proximally it is bordered on each side by a low membranous fringe with a lobulate free margin. The area between the fringes is comparatively smooth, but its surface is irregularly marked with rounded papillæ, and a few smooth ridges and five circumvallate papillæ, irregularly arranged in a $\wedge$ and asymmetrical, are obscurely traceable. The rest of the upper surface is entirely and thickly covered with small overlapping denticulate scales, each scale being the backwardly-directed distal end of a papilla, the proximal portion of which is a thick, short vertical column. The tongue of *Lyncodon* seems to resemble that of *Mustela* in all essentials, athough the posterior fimbriated crest seems to be better developed and the rounded papillæ amongst the denticulated papillæ seem to be fewer in number. But the examination of more material is required to establish these inferences (text-fig. 52, D–F, p. 1088).

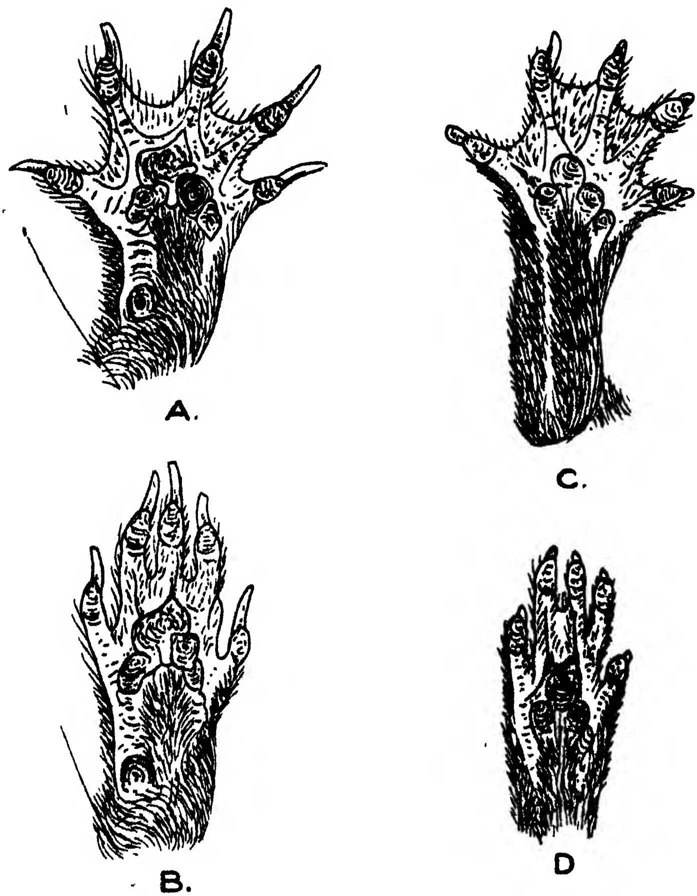
### *The Feet* *.

My description of the feet taken from the dried skins was erroneous in some respects. In the fore feet, for instance, the interdigital webs are better developed than was stated, but they are at the same time poorly developed as compared with other genera of the family, a considerable portion of the distal end of the digits being free. The foot also is asymmetrical. If the main axis be taken between digits 3 and 4, digit 2 does not form a symmetrical pair with digit 5, but is situated considerably in front of it, the 5th digit pairing in position with the 1st. Thus the fore foot in the disposition of its digits is very like that of *Ictonyx*, *Spilogale*, and *Mephitis*,

* The claws in this specimen are shorter than is usual for the species. But Col. Knight had it alive in Bonifacio and kept it in a tin, and since it was very restless and active, it is quite likely that the claws were worn down by the efforts the animal made to escape.

figured on pp. 821 and 824 of my paper, where it may be seen that the middle line of the foot was taken through digit 3, and that the digits show perissodactyle symmetry, instead

Text-figure 53.




A. Right fore foot of *Lyncodon* with the digits spread.
B. The same with the digits nearly in contact.
C. Right hind foot of the same with the digits spread.
D. The same with the digits nearly in contact.

of the artiodactyle symmetry exhibited by *Mustela*, *Martes*, and others; and it is interesting to observe that the genera with perissodactyle symmetry are fossorial, long-clawed forms, whereas the genera with artiodactyle symmetry are short-clawed, cursorial

or scansorial forms. *Lyncodon* is one of the few genera of the family which combines musteline elegance of shape with longish or long fossorial claws, and the fore foot very markedly approaches the perissodactyle type.

The digital pads are striolate and irregularly roughened, as also is the plantar pad. In the latter the four interdigital elements are clearly distinguishable, the median element or lobe being much the largest and obliquely set. On the outer side of the foot a naked tract of corrugated skin extends backwards from the external lobe of the plantar pad to the rounded striolate carpal pad, which is single, no trace of the inner carpal element being observable. There is a similar but shorter naked tract of skin behind the posterior (pollical) element of the carpal pad; but the median area of the skin between the plantar and carpal pads is hairy. The sole of the foot immediately round the plantar pad is naked; but the lower sides of the interdigital webs and the sides of the lower surface of the digits are sparsely hairy, the hair growing in very definite isolated tufts. The carpal vibrissæ are reduced to a single long bristle (text-fig. 53, A, B, p. 1090).

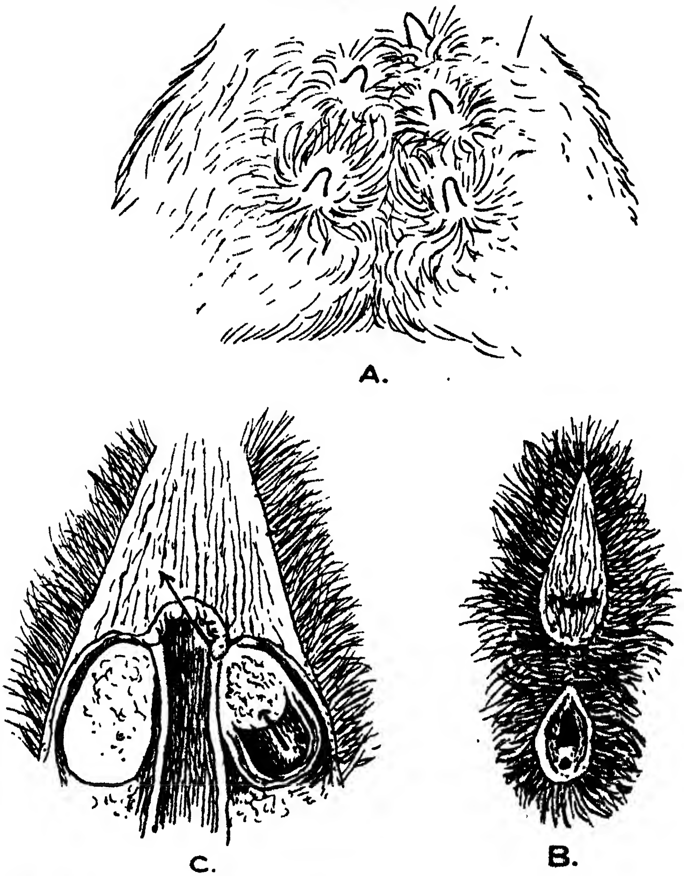
The hind foot is smaller than the fore foot, and has the 2nd, 3rd, and 4th digits webbed to the proximal ends of the digital pads, and the 2nd and 3rd and the 3rd and 4th are more closely tied together than in the fore foot. The 4th digit is slightly longer than the 3rd, and the 3rd than the 2nd; but as in the case of the fore foot, these three digits are closer together than the 4th is to the 5th. The webs between the 4th and 5th and between the 1st and 2nd are about as deep as the corresponding webs on the fore foot: and, as in the fore foot, digits 2, 3, 4, and 5 are not so symmetrically disposed in pairs as they are in *Mustela* and other active cursorial members of the family. The lower sides of the webs are hairy to about the same extent as in the fore foot, and the area in front of and at the sides of the plantar pad is similarly naked. The plantar pad is four-lobed. The inner or pollical lobe is small and not very clearly defined, but the other three are sharply differentiated and subequal, and alike, much more so than in the fore foot, all having convex edges, the median not being much broader than the laterals. In the concentric arrangement of their ridges they are also more like the lobes of the plantar pad of *Mustela*, the irregular shape of the plantar pad of the fore foot recalling that of such fossorial forms of the family as *Meles* and *Taxidea*. There is no trace of metatarsal pads, the entire metatarsal area being covered with hair from the heel to the plantar pad, except for an ill-defined nearly naked strip extending proximally from the base of the 5th digit behind the outer lobe of the plantar pad (text-fig. 53, C, D, p. 1090).

### *The Anus and External Genitalia.*

The *Anus* opens on the lower anterior portion of a naked lanceolated area of skin which is narrowed and pointed where

it passes on to the root of the tail and convexly rounded at the opposite end towards the vulva. Just within its orifice opens the pair of anal glands, which are tolerably large and oval and constructed as in other Mustelidæ, consisting anteriorly

Text-figure 54.



A. The mammæ of *Lyncodon*.

B. The anal and genital area of the female *Lyncodon*.

C. Dissection of the anal area showing the two anal glands, the gland on the right of the figure cut open, with a bristle, indicated by the arrow, passing from the storage sac through the secreting portion to the exterior.

of a muscular sac and posteriorly of a thickened glandular portion traversed by a narrow duct through which the secretion passes, when ejected, from the storage sac to the external orifice (text-fig. 54, B, C).

The perinæum is short and hairy, and the *vulva* is piriform, with the urinary orifice opening just below the orifice of the vagina (text-fig. 54, B, p. 1092).

From the size and structure of the anal glands it cannot be doubted, I think, that their secretion is offensive as the secretion is known to be in *Grisonella*, *Grison*, and *Mustela*. And the genus has the type of colouring, grey above and black below, found in *Grison* and *Mellivora*, in which the scent of the secretion is peculiarly offensive and nauseous. In the case of *Lyncodon*, too, there is a broad, conspicuous white band upon the head, and there is no doubt that the genus is warningly coloured. There is a similar but less conspicuous frontal band in *Grison*, and the two genera are very much alike in colour. I discussed this resemblance in my paper upon warning coloration in Musteline Carnivora (Proc. Zool. Soc. 1908, p. 953), and having no evidence that *Lyncodon* was offensive, I suggested that the likeness might be an instance either of Batesian mimicry or of Müllerian resemblance. The evidence now to hand that *Lyncodon* is probably as nauseous as *Grison* will bring the case into the latter category.

In accordance with the general rule that fertility is a measure of mortality, species which are especially protected produce a comparatively small number of young in a season. In this connection it is interesting to note that the example of *Lyncodon* here described has only 5 inguinal mammæ, 2 on the left side and 3 on the right (text-fig. 54, A, p. 1092). This suggests that the litter of young is smaller than in our species of Mustelidæ (*M. erminea*, *nivalis*, and *putorius*), which, typically at all events, have 8 mammæ to accommodate their young. In the case of *M. erminea* as many as 10 young to the litter have been recorded.

### *The Auditory Bulla.*

Owing to lack of material I was unable to describe in detail the structure of the tympanic bulla when I wrote my paper on this portion of the skull in the Mustelidæ (Proc. Zool. Soc. 1921, pp. 483–484). All that it was possible to record was that "a skull of *Lyncodon*, with a broken bulla, in the British Museum shows that the cavity is broken up by trabeculæ into spaces which extend into the mastoid. It is not possible, however, to ascertain from this specimen whether the cavity before fracture was divided by a partition into two chambers as in *Grisonella* or not." The fresh specimen confirms the first part of this observation, and shows that the posterior portion of the cavity of the bulla freely communicates with the hollowed mastoid portion of the periotic, the wide passage lying just externally to the petrous portion of that bone as in *Grisonella*; and also that the floor of this portion of the cavity is irregularly pitted by the anastomosis of bony ridges, and that the roof

of the bulla is depressed and confluent with the tympanic ring throughout its extent. There is, however, no trace of the large arched rafter which in *Grisonella* descends just behind the tympanic ring to the petrous bone and divides the cavity into an anterior and posterior chamber communicating by a narrow passage just above the periotic. The cavity, therefore, is undivided as in *Mustela* Furthermore, the roof of the bulla is thickened and permeated by air-cells as in *Mustela*; but the bone is not so thickened as in that genus, and the air-spaces are larger and do not present the spongy appearance characteristic of *Mustela* as described and figured in my previously quoted paper.

The bulla of *Lyncodon* thus shows resemblances to that of *Mustela*, and differences from that of *Grisonella* in the absence of the partition and the thickening of the roof and the number of air-cells in it, there being only a few in *Grisonella*; but it resembles the bulla of *Grisonella* and differs from that of *Mustela* in that the posterior portion of the cavity communicates freely with the hollowed mastoid, and has its floor pitted by the anastomosis of bony ridges. And it resembles the bullæ of of both these genera in the complete confluence of the tympanic ring with the roof of the bulla (text-fig. 52, A, p. 1088).

So far as this portion of the skull is concerned, *Lyncodon* might be described as intermediate between *Mustela* and *Grisonella*.

## 55. A Note on an Albino Grass-Snake. By JOAN B. PROCTER, F.Z.S., F.L.S., Curator of Reptiles.

[Received October 11, 1926: Read October 19, 1926.]

(Plate I.)

Albinism in Mammals and Birds is comparatively common, but in Reptiles it has only been recorded in a few isolated instances. In the case of the Ophidia, Mr. Boulenger has observed that "partial albinism is rare; perfect albinism, characterized by absence of black pigment in the eye, rarer still." * In certain species a pallid ivory tint is normal. In the Tree-Boa *Chondropython viridis* the young snake may be very pale yellow or pink, but is most frequently cream-colour. The green colour subsequently appears surrounding white spots, and ultimately spreads until green is the ground-colour in the adult Boa. In this case, therefore, pigment develops late in the life-history. Many desert species are pale silver-sand-colour, such as *Cerastes vipera*, *C. cornutus*, and *Crotalus mitchelli* which is sometimes called the "White Rattlesnake," but no cases of albinism have been recorded in these species.

True albinos have been known in the Grass-Snake, *Natrix natrix*, but the young specimen at present living in the Reptile House is such a perfect example, that the Garden Committee of the Society commissioned Mr. Green to make a water-colour drawing of it in order to have a permanent record of its tints in life, which will of course be destroyed by death. (Plate I.)

For the gift of this little snake we are indebted to Mrs. Durtnell, who, although thinking that it might be a viper, caught it uninjured and brought it to the Gardens in perfect condition. Its ground-colour is ivory-white, with a slightly creamier tint on the præfrontals, internasals, and first few labials. This same tint is repeated in the collar where, in a normal specimen, the yellow patches would occur. Wherever there should be black pigment, that is to say the collar, lateral spots, and ventral checkerings, the skin is as transparent as gauze, showing the colour of the muscular coat through. This is the palest mauve-pink, and produces a very odd effect, especially on the ventral surface where the liver, and other organs, show through the pale semi-transparent flesh. The characteristic collar on this white snake is therefore shown up in cream and pale mauve-pink.

The eyes have brilliant dark red pupils, surrounded by a more opaque pale orange iris, and entirely lack that dull, blind look seen in pink-eyed mammals. The nostrils show up their pink linings, and the tongue is pink at the base and ivory

* Boulenger, G. A. 'The Snakes of Europe,' 1913, p. 39 (Methuen, London).

on the bifurcated portion. The general effect is very pale and fragile like carved ivory, with jewel eyes.

This is the second albino snake which has been on view in the Reptile House. The first, an Indian Cobra, *Naia tripudians*, was a true albino in the black pigment sense, but had a powdering of sand-coloured chromatophores on the hood, forming shadowy white "spectacles" on a sandy ground-colour. An account of this snake, together with a photographic plate, appeared in the Proceedings in 1924 *, and it lived in perfect health for 22 months. During this time we were fortunate enough to obtain an excellent cinematograph record of it, taken out of doors in natural surroundings, and a copy of this film is preserved in our library.

Most of the albino snakes have this trace of sandy or cinnamon coloured pigment emphasising the markings characteristic of the species. Mr. Walter Goodfellow has seen a white Reticulated Python with faint markings of this kind, and with red eyes, in Singapore. Other records are as follows:—Ditmars †, in 20 years, has seen an albino Palm Viper, a Rattlesnake (species not indicated), a Milk Snake, and a Black Snake. Klauber ‡ has published a photograph of an albino Gopher Snake, and Boulenger §, in 'Snakes of Europe,' mentions the Grass-Snake, Tesselated Snake, Æsculapian Snake, and Smooth Snake.

* Procter, J. B., P. Z. S. 1924, p. 1125, pl. i.
† Ditmars, Zool. Soc. Bull., New York, xxiv. no. 6, 1924, p. 127.
‡ Klauber, Zool. Soc. Bull., New York, xxvii. no. 3, 1924, p. 80.
§ Boulenger, 'Snakes of Europe,' 1913, p. 39.

## 56. Some Notes on the recent Birth of a Hippopotamus (*H. amphibius*) in the Gardens. By G. M. Vevers, F.Z.S., Superintendent.

[Received October 17, 1926: Read November 2, 1926.]

(Text-figures 1, 2.)

Young Hippos have been born in the Gardens on four previous occasions, but only one of these was reared and reached maturity: this was the famous "Guy Fawkes" which was born on November 5th, 1872, and lived for 36 years in the present Hippo House. Two others, one born in February 1871 *, the other in January 1872, lived only a few days, and the fourth, born in September 1925, died at birth.

A. D. Bartlett, who was Superintendent at the time, gave detailed accounts of two of the three early births in the Proceedings of the Society †.

The one born in September 1925 was approximately six weeks premature, the period of gestation, as calculated by Keeper E. Bowman, being 200 days as against 240 days for full time. Further evidence of this was afforded by the state of the nails, which were gelatinous and very much longer than they are normally at birth. The presentation was abnormal, and, it being her first confinement, the mother was in great distress. She plunged into deep water and the young one was born almost immediately, but being attached to the female by the umbilical cord it was pulled under and drowned. At this time the mother, "Joan," was only 6 years old.

On enquiry it was found that at the Zoological Gardens in Philadelphia, where several young Hippos have been successfully bred, the pond was only four feet deep and when a confinement was expected, the floor was built up with heavy timbers so that the depth of water was about 12 inches, and in this shallow pool the young were born.

In Amsterdam, where "Bobbie," the father of the present baby, was born, the mother is given free access to the pond which is several feet deep, but the birth always takes place on land, the level of the water being almost up to the floor of the sleeping den so that the young one can easily get in and out.

Soon after the birth of the premature calf last year, the pond in the Hippo House, which was 7 feet deep, was filled up so as

* There is a cast of this animal taken after death on the wall of the Giraffe House.

† P. Z. S. 1871, p. 255 *et seq.* P. Z. S. 1872, p. 819 *et seq.*

to leave a depth of 4 feet of water, and the steps leading down into the pond were made much shallower.

Two months before the last confinement was expected, the female was screened from the public and shut away from the male. The night before the birth took place, Bowman, noticing that she appeared uneasy, shut her away from the pond and put down an extra large bed of straw which she proceeded to take up in her mouth in small quantities, dip in her drinking trough and spread all over the floor of the sleeping den. Labour

Text-figure 1.

The fore foot of the premature Hippo calf born in Sept. 1925, showing the long gelatinous nails which are not present at birth.

commenced at 6 A.M. on the following morning (August 20th), after 241 days of pregnancy, and 5 hours later, at 11 A.M., a young male was born.

The mother and young were left undisturbed until 7.30 P.M., when the sliding door leading to the pond was raised and the mother went down into the pond, which was full of warm clean water. The young one followed immediately, shuffling along on his knees, as he was unable to walk. As soon as he was in the water he seemed more at home and began to swim up and down the pond, but every time he ventured out of his

depth the mother tried to raise him on her head. After a short time, the mother submerged her body entirely, turning on her side, and the young one began to suckle under water, coming up to breathe at intervals of about 20 seconds. This suckling under water still continues, and the calf has not been seen to suckle on land although he was able to walk and follow his mother out of the pond on the fifth day after birth. The average time the young one remains under water is 40 seconds, although on occasions he has been timed to remain under for as long as 3 minutes. The average time which adult hippos, in our Collection, remain under water without breathing is minutes.

Text-figure 2.

**Young Hippo at 3 weeks and mother.**

Bartlett records that "Guy Fawkes" was observed on one occasion to submerge for 15 minutes a few days after birth, and that, although suckling took place under water at first, it also took place on land, the mother standing and arching her back slightly. In both cases which he describes the young one was able to walk at birth, whereas the present one could not do so for five days. This might have been due to muscular weakness, which, however, did not prevent him from swimming well.

Dr. C. Kerbert of Amsterdam gives the period of gestation as 234 days; Bartlett records 237, 227, and 242, the last being

in the case of "Guy Fawkes," there being only one day's difference between it and the one born last August.

At birth the general resemblance the young one bore to the Pigmy Hippopotamus (*C. liberiensis*) was notable, especially about the contour of the head; the nostrils and eyes being much less elevated than in the adult *H. amphibius.*

The conclusions to be drawn from the above observations are:—

(1) The period of gestation is approximately 240 days.

(2) In nature the young one is probably born in a bed of reeds close to the edge of the water, or in very shallow water.

(3) The young is able to swim before it can walk.

(4) Suckling normally takes place under water.

(5) In captivity it is of the utmost importance to shut the female away from the male and from the public for at least one month before confinement takes place: also the level of the water in the pond should be almost the same level as the floor of the sleeping den.

(6) The Pigmy Hippo is the more primitive of the two races.

# 57. The Land and Freshwater Mollusca of the Scilly Isles and West Cornwall. By O. W. Richards, B.A., and G. C. Robson, M.A., F.Z.S.*

[Received June 15, 1926: Read November 2, 1926.]

(Text-figure 1.)

Contents.



## 1. Introduction.

In July 1925 a visit was paid to St. Mary's, the largest of the Scilly Isles, and to the Land's End district of West Cornwall, and a comparative study was made of the land and freshwater Mollusca collected on an intensive scale during the trip. The results of this study are presented in this paper along with certain general considerations. Another paper is being prepared in which the forms obtained at some 120 stations are listed together with the names of the associated plants and other data.

The object of this survey was to ascertain to what extent the Molluscan fauna of a group of coastal islands in the Temperate Zone has diverged from that of the adjacent mainland during its period of isolation. No intensive work on the mollusca of small islands off the British coasts has been undertaken on a comprehensive scale, though the Clare Island Survey (Stelfox, 1912) gives a detailed list of occurrences and habitats, and small collections have been made on many Hebridean and other islands. Some attention has been paid to the statistical study of isolated colonies of British land snails (*e. g.* on different walls) by Boycott (1919).

* The last-named author's work is offered for publication by permission of the Trustees of the British Museum.

There is no need at the present time to discuss the importance of geographical and habitudinal isolation in promoting evolutionary divergence. We are, however, in need of a more intimate acquaintance with the details of the process. Thus we require information as to (1) the rate at which isolated faunas diverge, (2) whether all the species of an isolated fauna tend to diverge at the same rate, (3) the extent to which divergence between two isolated faunas having a common origin depends on the occupation of ecologically distinct habitats. Whenever we take up the study of the fauna of areas in which much local isolation and racial differentiation is found, we sooner or later encounter apparently paradoxical phenomena. No species or varieties of land Mollusca have been recorded as peculiar to the Inner and Outer Hebrides*, which have been the seat of intensive diversification of small mammals, and even among the latter, some varieties range over many islands, while others are restricted to single islands. These are problems which may be answered at present only by making valueless assumptions about the date of separation, responsiveness to environmental conditions, and so on.

It seemed therefore desirable to make an intensive survey of the mollusc fauna of an island or group of islands not too far removed from the British Coast, the ecological conditions characteristic of which could be fairly readily ascertained, and about the separation of which from the mainland some information was reasonably to be expected. It was moreover necessary to select an island associated with a definite area of adjacent mainland, the local fauna of which was fairly well known. For reasons given elsewhere (Richards & Robson, 1925, p. 641) the Scilly Isles were selected.

It became apparent that the first visit must be in the nature of a reconnaissance for the following reasons. A. It was obviously necessary to ascertain if the Scillies were in general suitable for such a study, both from the point of view of the facilities for work and the nature of the fauna. B. It was necessary to make preliminary collections *en bloc* in order to see if there were any noticeable divergences both in structure and habitat-occupation before settling down to study particular species intensively. C. It was felt that, as much attention would have to be paid to the study of homologous habitats occupied on the island and the mainland, a preliminary study of these would be necessary for formulating an ecological technique suitable for the occasion. The results attained in 1925 are therefore of a preliminary nature; but as they already throw some light on the problem of insular divergence, it is considered desirable to publish them. They include (1) the proof that of the 39 species found by us (of which 15 are new "records"), twelve show differences from the

* No such local forms have been recorded up to date, though many islands have been visited by the field collector. In the absence of an intensive survey we do not assert that there are no such local forms.

mainland forms, though the significance of such differences is doubtful at present, while twenty-seven are apparently unmodified; (2) an analysis of the habitats occupied in St. Mary's and West Cornwall and of the distribution of the various species therein; (3) a summary of the general ecological conditions characteristic of the two areas and an examination of the extent to which they differ.

Our thanks are due in the first instance to the Government Grant Committee of the Royal Society and the Committee of the Godman Exploration Fund for financial assistance. An early acknowledgment of the help received from various quarters in promoting this survey has already been made (Richards & Robson, 1925). From this acknowledgment we regret that the name of Mr. G. W. Gibson was omitted. We now take the opportunity of thanking those specialists whose names will be found associated with reports on particular species included in the text, and Dr. G. Glasspool of H.M. Meteorological Survey, Miss E. L. Hendricks and Mr. A. J. Wilmott for assistance rendered in special points. Messrs. A. E. Stelfox and R. Winckworth took much trouble in studying our species of *Pisidium* and *Goniodiscus*, though their results are not included here, being negative as far as significant divergence is concerned. It is hoped, however, to publish their notes elsewhere.

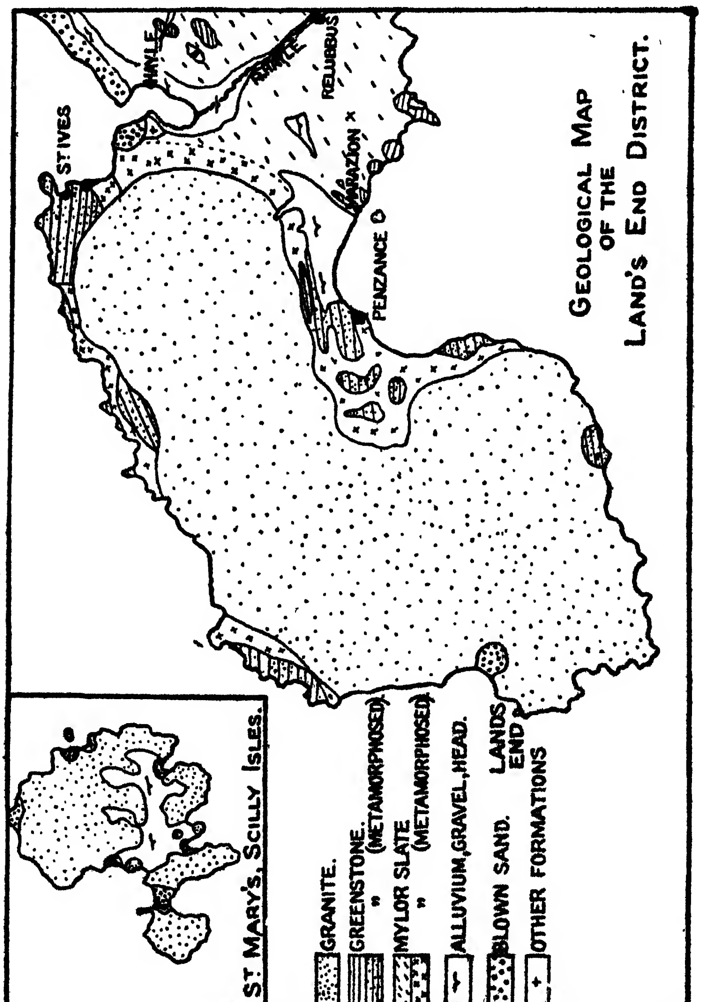
## 2. The Physiography and Ecological Conditions of St. Mary's and Land's End.

The area investigated consisted of the whole of the island of St. Mary's, including Toll's Island, a rocky heather-covered islet on the N.E. side of the latter, and the Land's End peninsula west of a line drawn from Lelant Golf Links (on the west side of the River Hayle) to the farm buildings known as Tregambo, half a mile S.E. of Relubbus and thence back to St. Michael's Mount In the course of this report the Scilly area is referred to as "St. Mary's" and the Cornish area as "Land's End." The latter is smaller and ecologically more homogeneous than either the "West Cornwall" of the Conchological Society's Survey (Roebuck, 1921) or the "Land's End" of Davey's 'Flora of Cornwall' (1909, p. lxix).

1. The Land's End area consists of two rather sharply contrasted areas. West of a line drawn from Lelant to Penlee Point (just S. of Penzance) is a mass of granite fringed here and there by metamorphosed diabase and slates of the Mylor series. This forms the characteristic Land's End massif, a high undulating tableland of heather country, rising in places to over 800 feet in height. Eastwards the land sinks to the valley of the Hayle and Marazion marshes, where the unmodified Mylor slates and alluvium yield arable, marsh and wooded country attaining a maximum height of about 280 feet. Patches of unmodified diabase occur round Penzance, St. Ives, etc. The distance from

the mouth of the Hayle to Marazion is just over five miles; from St. Ives to Land's End about fifteen miles, from Penzance to Cape Cornwall about eight miles.

Text-figure 1.




2. St. Mary's is separated from Land's End by a channel some twenty-eight miles in width. The average depth of this channel on the direct line between Land's End and St. Mary's is about 36 fathoms, and all the islands lie within the 40 fathoms

contour. The channel is very uniform in depth; but for the sake of future reference we must note that the following shallows occur:—the Longships (2 fathoms), a short distance from Land's End; Carn Base (9 fathoms), a little farther westward; an unnamed bank (24–28 fathoms) about half-way across to Scilly; and the Seven Stones (5½ fathoms) about six miles from St. Martin's. Cape Cornwall Bank (15 fathoms) and the Wolf Rock lie a little to the north and south respectively of the main line. Topographically considered the islands lie at the extremity of a spur marked by the 40 fathoms contour, which runs out from the West of England massif. The Cornish peninsula and this submarine spur seem to be part of the same topographical feature.

St. Mary's consists of two masses of granite joined by a low ridge of blown sand. In the 18th century Hugh Town, which stands on the ridge, was subject to flooding by the sea, but recent elevation seems to have removed this danger. The island contains, in addition, deposits of "Head" (decomposed granite), a little Eocene (?) gravel and alluvium. There are no Palæozoic rocks or diabase such as we find in Land's End. The granite, however, seems to be identical with that of the latter. The greater part is coarse-grained and porphyritic, only three small patches of a fine-grained type occurring. The island measures about $2\frac{1}{3} \times 2\frac{1}{3}$ miles and its highest point is 166 feet above sea-level. The following data should be noted.

| | St. Mary's. | Penzance. |
|---|---|---|
| *Rainfall* (average annual) ... | 31·87 in. | 40·93 in. |
| *Atmospheric humidity* (average monthly 1922: 3 daily observations) ... | 89–84–89 | 79–?–78 |
| *Temperature.* | | |
| Mean temperature for year:— | 52°·2 † | 52°·6 * |
| Mean of maximum ... | 56°·0 | 63°·7 |
| " " minimum ... | 48°·3 | 39°·3 |

* 1896–1925. † 1881–1915.

### *The Effect of Spray.*

In an island of relatively slight elevation, such as St. Mary's, the effect of spray must be of considerable importance, though we are unable to trace any structural or other peculiarities in the fauna directly to this cause, nor are we able to define the amount of spray-borne chlorine that is found in the soil of the island. Irwin (1920, p. 276) found the following figures for Cumberland:—

| Locality and distance (in miles) from sea. | Parts NaCl per 1,000,000. (Oct.–Dec.) |
|---|---|
| Maryport (0).................... | 199 |
| Cockermouth (6½) ............ | 37 |
| Dungeon Ghyll (15)........... | 15 |

Martin (1925) found that dew-ponds on the Sussex downs at a height of 500–800 feet get 12·2 parts of chlorine per 100,000 parts. Neither in St. Mary's nor in "Land's End" is any place visited by us over four miles from the sea, and the majority of island and mainland stations are within one mile of the sea, so that we do not think any structural differences that may occur between the mollusca of the latter are to be attributed to this factor.

*Vegetation, etc.*

In Davey's 'Flora of Cornwall' (1909, p. lxix) the Scillies are treated as part of the Land's End botanical division of Cornwall. For the purpose of an intensive survey this grouping is valueless. It may be true that all the plant species which occur on the islands are likewise found on the mainland, but we require to know to what extent the total mainland flora is represented on the islands. Davey's district, as pointed out above, is larger than our "Land's End," as it includes all the county west of a line drawn from Hayle through Praze and Sithney to Porthleven.

As far as we can ascertain the flora of the islands consists of 481 species and varieties, of which 348 were recorded by Townsend (1864), 25 by Lawson (*cf.* Marquand, 1893), 44 by Somerville (1893), and 64 by Marquand (1893). The Land's End flora consists of 879 species (Davey, *l. c.*). Even if we make some allowance for the lack of attention paid to the islands and for the larger size of Davey's "Land's End," the difference is still very marked. It is very noticeable in the case of trees. On St. Mary's the elm, apple, pear, and ash (the latter a recent introduction) only are known. Only one plant is recorded from Scilly which does not occur in Land's End, viz. *Arthrolobium ebracteatum*. This is otherwise found in the Channel Islands and France.

Of the animals important in the molluscan food-cycle not a great deal can be said at present. The *birds* have been recorded by Clark and Rodd (1906), from whose account we may note some points. The Jay is absent and the Cuckoos are more common in the breeding season than in Cornwall. Apparently certain forms are on the decrease, *e. g.* the Roseate Tern, the Common Tern, and the Black-backed Gull, while the Linnet is on the increase (Robinson, 1914, p. 144). While the sea-birds are not of immediate significance in the molluscan food-cycle, it is important to note the great number of Puffins and Shearwaters. Certain exceptional visitors such as the Golden Oriole occasionally nest in the islands. Clark and Rodd do not comment on the lack of trees as a factor in the bird-life, but we suspect that the resident species are partly limited by this. Robinson (*l. c.* p. 117) notes that the broods of the Song-Thrush are distinctly below the average in number; but he gives no figures for Cornwall.

Though the Scillies are unique in possessing a species of the genus *Crocidura*, the white-toothed Shrew, which is otherwise not recorded from the British Isles, the islands seem to be poor

in small mammals *. Beyond the Common Rats and House-Mouse and the ubiquitous *Apodemus sylvaticus* there are no others. No Voles have yet been recorded. We are unwilling to consider that they are definitely absent; but certainly no records are available up to date. Of the other groups important in the molluscan food-cycle the predaceous beetles are very poorly represented according to my colleague Mr. K. G. Blair's experience, the common snail-eating *Cychrus* being absent though represented in Land's End. Mr. Blair considers that these beetles are limited by the absence of wood-eating insects, which is referable to the lack of trees.

The main ecological differences between St. Mary's and Land's End may thus be summarized:—(1) The climate is more equable in Scilly. (2) The latter has a distinctly lower rainfall; but the atmosphere is more humid. (3) Geologically St. Mary's is similar to the Land's End massif; but it lacks the slate and diabase found adjacent to the granite in the latter. (4) The whole of St. Mary's probably receives a considerable amount of spray-borne chlorine. This would be found also in Land's End, diminishing only slightly in the parts most remote from the sea. (5) The differences in vegetation are uncertain; but there is a noticeable poverty of trees in St. Mary's. (6) Of animals important in the molluscan food-cycle small rodents and carnivorous beetles are very poorly represented in St. Mary's. In the case of one species of snail the presence of a species of *Crocidura* may be important. The avifauna seems to present certain special problems; but its relation to the mollusca is as yet uncertain.

### 3. The Mollusca of West Cornwall and Scilly.

The Census of British Land and Freshwater Mollusca (Roebuck, 1921) published by the Conchological Society gives a total of 25 species from the islands and 74 from West Cornwall. In the same year two more records were added to Scilly (*Hyalinia draparnaldi* and *Helix aspersa*), making the total 27. As previously stated "West Cornwall" of this list is a much larger area than our "Land's End," including as it does the area west of a line drawn from Truro to St. Columb.

The following is a complete list of Scilly and Land's End records brought up to date, the total for St. Mary's being made up of 27 species already recorded and 15 (? 14) new records. One new record was obtained in Land's End.

#### (a) *St. Mary's*.

(New records indicated by asterisk; species not obtained by the survey of 1925 in square brackets; number of stations at which the species were obtained in 1925 in round brackets.)

* Small mammals, especially rats, mice, and voles, are of importance in Molluscan ecology, as they certainly prey on snails. One of us (O. W. R.) obtained definite evidence that *Crocidura* feeds on *Helicella virgata*.

[*Testacella maugei.*]
*Limax maximus*, typical (1).
„ „ var. *cellaria* (9).
„ „ „ *sylvatica* (2).
„ *flavus* (6).
„ *arborum* (1).
*Agriolimax agrestis*, typical (18).
„ „ var. *reticulata* (1).
„ „ „ *pallida* (2).
„ *levis* * (1).
*Milax sowerbyi* (10).
„ *gagates* * (5).
*Vitrina pellucida* * (3).
„ „ ? new variety (1).
*Hyalinia nitidula* (14).
„ *cellaria* * (12).
„ *draparnaldi* (12).
„ *alliaria* (1).
„ *radiatula* * (1).
*Arion ater*, typical (1).
„ „ *cinereo-olivacea* (1).
„ „ *rufa* (1).
„ „ (1).
„ „ *marginata* (3).
„ „ *marginella* (3).
„ *subfusca* * (5).
*Arion hortensis* * (1).
*Goniodiscus rotundatus* (11).
*Helicella virgata* (3).
[ „ *itala*.]
„ *caperata* (5).
*Cochlicella barbara* (6).
*Ashfordia granulata* (5).
*Hygromia hispida* (1).
„ *striolata* (3).
„ *revelata* (3).
*Vallonia excentrica* * (1).
*Helix aspersa* (21).
*Cepea nemoralis* (9).
*Cochlicopa lubrica* (7).
*Lauria cylindracea* (7).
*Vertigo pygmæa* * (3).
*Balea perversa* (3).
*Succinea pfeifferi* *† (2).
[ „ (?) *elegans*.]
*Limnæa truncatula* * (4).
„ *pereger* (5).
*Planorbis leucostoma* (8).
*Pisidium casertanum* * (3).
„ *personatum* * (3).
„ *milium* * (1).
„ *obtusale* * (3).

† We follow some recent authors in regarding *S. elegans* and *S. pfeifferi* as different species.

All these species except *Testacella maugei*, *Hyalinia radiatula*, *Pisidium milium* and *personatum* were found by us in Land's End, and the following forms occur in the "West Cornwall" of the Census, but not in Scilly. Species not obtained by us in Land's End are indicated by brackets and new records for Cornwall by an asterisk:—

(*Hyalinia crystallina*).
( „ *rogersi*).
( „ *pura*).
*Euconulus fulvus* * (3).
*Zonitoides excavatus* (7).
( „ *nitidus*).
*Arion intermedius* (1).
„ *circumscriptus* (3).
*Punctum pygmæum* (1).
(*Pyramidula rupestris*).
(*Hygromia fusca*).
(*Acanthinula aculeata*).
*Vallonia pulchella* (1).
(*Arianta arbustorum*).
*Cepea hortensis* (4).
(*Euparypha pisana*).
(*Ena obscura*).
(*Azeca tridens*).
(*Pupa marginata*).
( „ *secale*).
*Clausilia bidentata* (12).
(*Carychium minimum*).
(*Phytia myosotis*).
(*Ovatella bidentata*).
*Ancylus fluviatilis* (2).
*Limnæa palustris* (1).
( „ *glabra*).
(*Planorbis albus*).
„ *nautileus* (1).
(*Aplexa hypnorum*).
(*Paludestrina ulvæ*).
(*Bithynia tentaculata*).
(*Valvata piscinalis*).
(*Cyclostoma elegans*).
(*Pisidium amnicum*).
„ *nitidum* (1).

Three species—*Hyalinia radiatula*, *Pisidium milium* and *personatum*—are thus recorded from Scilly but not from West Cornwall. These species are recorded elsewhere in England.

From a consideration of these lists it will appear that, as compared with the "West Cornwall" of the Census, the fauna of St. Mary's is very impoverished as it possesses 42 species as opposed to 75. If we restrict the Cornish area to Land's End, as defined herein, the poverty of St. Mary's is far less marked, for

we obtained only 50 species in "Land's End" as compared with the 42 of St. Mary's. We are unwilling to express an opinion as to the precise number of species actually found in the Land's End area as defined by us. The Hennels (1848) recorded 48 species from the neighbourhood of Penzance. Marquand's list for West Cornwall (1884), which includes the country as far east as Falmouth, does not specify localities with enough accuracy to be of any use. There are several recent papers on small collections from Land's End, but no exhaustive lists. We are inclined to believe that our collections represent approximately the numerical relationship of the St. Mary's and Land's End areas, and that the latter is only a little richer in species than the former.

(b) *Comparison of Scilly and Land's End forms.*

The specimens obtained from the two areas were examined with a view to finding out if the insular forms show any difference from those of the mainland. It seemed likely that if any differences occurred they would be slight "statistical" ones, the significance of which could only be assessed by a specialist or by a student having at his disposal a large amount of varietal material. It would not be enough to examine specimens from Land's End alone; for a variant living on St. Mary's might conceivably be absent from Land's End but be found elsewhere in the West of England. If the St. Mary's forms showed any differences from those of Land's End it would be part of the task to show whether such variants are (1) new forms not found elsewhere, or (2) rare variants missing from W. Cornwall but occurring elsewhere. In the present report it is obviously impossible to give a final answer to these questions, though we may go some way towards doing so. The examination made has been purely a conchological one except in a few cases. However desirable it may be that we should know something about the variation of other forms, it is manifestly impossible to use such data profitably in this particular case, as the bulk of our present knowledge of the variation of British and Continental land molluscs rests on conchological data.

The result at which we have arrived after an examination of our material is as follows:—(1) There are no forms of specific and probably none of varietal rank restricted to St. Mary's. (2) In a certain number of cases the Scilly forms exhibit characteristics not found in the mainland population or in such material from the British Isles and the Continent as we have been able to obtain. (3) These differences are of a slight order, except in two or three cases, and they will be subjected to a complete statistical study as soon as more material, both from St. Mary's and elsewhere, is available. (4) The differences that we are able to distinguish between the St. Mary's and the mainland population do not exceed in magnitude the differences usually found between colonies found in the same area, but not immediately adjacent one to another.

It is interesting to note that Blair (1925) records no local species or varieties of Lepidoptera from the Scillies. "Interesting variation" is recorded but no marked local races.

The following is a detailed examination of the species in which differentiation of the insular forms can be discerned. Twelve species are here involved. Of the remaining twenty-seven species a few (e. g. *Helicella caperata* and *virgata*) were not sufficiently adult to enable us to speak with certainty, and a few of the slugs owing to shrinkage and discoloration in the preservatives used were not in a fit state for highly critical work.

Vitrina pellucida.

Mr. B. B. Woodward reports:—"The specimens from the Scillies show a conchological difference from those of the mainland. The rate of increase of the whorls is less rapid than in the Land's End forms, and therefore the whole shell is more globular and the aperture rounder. . . . Some specimens in the collection of Dr. Boycott from Birdlip (Gloucs.) show a slight tendency to approach the Scilly specimens, but cannot be confused with them." This globular form is not unlike the variety *dillwyni* reported from Glamorganshire and a few Continental localities (Taylor, 1906). Comparison with the figure of that variety (as *V. ballardi*) given by Pollonera (1884) shows that the form of the aperture is different. *V. pellucida* seems to vary very little. Sundry varieties of dubious value have been described, of which a flattened form (*depressiuscula*) and the globose form (*dillwyni*) seem to be more constant. The St. Mary's shells approach the latter, but plainly are not to be identified with it. The available evidence goes to suggest that *dillwyni* is not an environmental form.

Only ten specimens were obtained, a number insufficient for a final opinion.

Ashfordia granulata.

The aperture is relatively and absolutely wider in the St. Mary's form, and certainly longer than in any specimen to which we have access. The Scilly specimens are smaller than those from Land's End.

Hygromia revelata.

While the colour and texture of the shells of the St. Mary's forms are exactly like those of the Land's End and other mainland races, the size and proportions of the apertures differ, being narrower and longer in the St. Mary's forms, while the last whorl in the latter is not so deep.

The animals from both areas are not as large as the average specimens from most areas, which usually attain a height of 5 mm. If the species is an "annual" and if, as Taylor (*l. c.* p. 40) suggests, it becomes mature in the autumn, then the size of

these examples would suggest that they are normal representatives of the annual population but not yet fully grown. Otherwise, in the absence of representatives of larger size we should have to infer that the species is stunted in St. Mary's and Land's End. Twenty-six specimens were obtained from St. Mary's, which are scarcely enough to decide whether the differences in the forms of the aperture are significant.

VALLONIA EXCENTRICA.

Mr. Hugh Watson informs us that while the specimens from the two areas are alike in most shell characters they are all more coarsely striate than is usually the case, and that this condition is far more marked in the case of the Scilly examples.

HELIX ASPERSA.

We are indebted to Captain C. Diver for a very detailed study of this form, of which we obtained 243 examples (57 adults and 186 young) from St. Mary's (19 *loci*) and 141 (110 adults and 31 young) from Land's End (20 *loci*). All the variations found on the mainland occur on the islands except band formula (12)0(45) which is rare and sporadic normally, while in addition var. *exalbida* (again very sporadic), two young examples of 1(23)05 and 1.345, two very thin-banded forms of 12345 and one example of 10300 were obtained on St. Mary's, none of which occur in the mainland sample. Captain Diver says "this crop of band mutations (particularly those of station 38) might possibly argue some disturbance [*i.e.* some hereditary or purely phenotypic difference], but there are no means at present of judging the frequency of such mutations in the population at large." In four sets of insular forms the shells are thinner than usual and more compact in shape. The *clathrata* and *flammea* types are both absent from the island and occur in the mainland sample, "though, if the specimens from the two areas were samples of the same population, only about one example would be expected among the 57 insular adults." To summarize Captain Diver's report, it seems that, as far as can be seen from the numbers available, (1) certain band formulæ absent from the mainland examples occur on St. Mary's and certain formulæ present on the mainland are absent on the latter, and (2) that in certain cases the insular forms differ in shape and thickness of shell, though (*a*) this is not a general peculiarity of the island forms, and (*b*) the shell of *H. aspersa* tends to become thin in other areas *.

VERTIGO PYGMÆA.

Only seven adult examples were obtained from St. Mary's and none from Land's End. The St. Mary's forms are compared with

* We are very sceptical as to the value of correlation between thinness of shell and lime-free soil. Taylor (1906, p. 253) records thick shells from the Millstone Grit and many of our Cornish *aspersa* and *nemoralis* from granite localities are thick and solid. (But see p. 1118.)

series from Clevedon (Somerset), Silverdale (Lancs.), Farmoor (Berks.), and Alfriston (Sussex).

Three characters were examined:—(1) the indentation of the lip; (2) presence or absence of the lower entocone; and (3) the relative proportion of the ectocones *a* (upper) and *b* (lower).

| | (1) | (2) | (3) |
|---|---|---|---|
| *Clevedon* .................. | Rarely strong. | Absent. | $b > a$. |
| *Silverdale* .................. | Never „ | „ | $b = a$ in 6/11. |
| *Farmoor* .................. | Feeble. | „ in 40/47. | $b > a$. |
| *Alfriston* .................. | ? | Present in 3/3. | $b > a$. |
| *St. Mary's* .................. | Variable, strong to weak. | Present in 6/7. | $b = a$ in 5/7. |

The number of specimens is very small and there are no Cornish specimens available. These results are included as demonstrating a possible difference from mainland shells in the combination of characters.

Limnæa truncatula.

The examples obtained on St. Mary's are decidedly larger in the body-whorl than any from Land's End and several other English localities. They are nearly approached by a collection from Brittany.

Succinea pfeifferi.

A good number was obtained from both localities, and the results of this comparison are very decisive.

This species is very plastic, and its relation to *S. elegans* is by no means well-defined. The St. Mary's race is, however, wider than any of the eight series containing specimens of the same length which we have examined, and the aperture is longer. While the aperture-shape is markedly different, the width of the shell is nearly approached by a form from Jersey.

Milax sowerbyi and gagates.

Although only a relatively small number are available the St. Mary's forms of the two species both differ in size, being larger than the Land's End forms by 3 mm. or more in each case. Mr. A. E. Ellis, who examined this material for us, discovered that all the specimens were sexually mature, so that we are inclined to think that the size-difference is not directly connected with difference in maturity.

Lauria cylindracea.

Seventy-three examples were obtained from St. Mary's and forty-two from Land's End. In addition Mr. A. E. Ellis kindly lent us series from Kelmarsh (Northants) and Llandough (Glamorgan). The St. Mary's forms are slightly smaller than the mainland forms and the length of the aperture is the only

character which was suitable for investigation. This proved to be relatively smaller in the St. Mary's shells than in any mainland set. A more interesting point was discovered in the course of measuring the length. The St. Mary's shells and those from Land's End each give a trimodal curve in respect of this character. But the modes of these curves are at different points in the two sets. This trimodality is probably not due to yearly growth, *i. e.* to the presence of individuals representing different age-groups, as no such trimodality was found in the Kelmarsh set, in which a unimodal curve was given; nor is a similar trimodality seen in the size of the mouth. It would seem then that in this character both the St. Mary's and Land's End *Laurias* contain the same number of varietal tendencies, though of a different order in each case. To explore this interesting subject more fully we must await the acquisition of more material.

Two characters were measured:—

(1) The length of the mouth ...... *b*.
(2) The total length .................. *a*.

| | | | |
|---|---|---|---|
| A. *St. Mary's* ......... | *b* gives unimodal curve at | 1·178 | mm. |
| | *a* ,, trimodal ,, ,, | 3·028 | ,, |
| | | 3·470 | ,, |
| | | 3·788 | ,, |
| B. *Land's End* .. ... | *b* gives unimodal curve at | 1·256 | mm. |
| | *a* ,, trimodal ,, ,, | 3·220 | ,, |
| | | 3·640 | ,, |
| | | 4·100 | ,, |

C. Llandough (a very small series). *a* varies from 3·716–4·213. [mm.

D. Kelmarsh...... *b* unimodal curve at 1·306 mm.
*a* ,, ,, ,, 3·472 mm.

Planorbis leucostoma.

A very plentiful supply was obtained in St. Mary's, but the species was very poorly represented in Land's End. We have had recourse to comparison with series from Cleveden, an unnamed locality in Somerset, Romsey, two French and one Swedish localities. Of these seven localities the St. Mary's forms are easily the smallest, averaging 3·31 mm. as opposed to 4·53 mm. from Cleveden, 5·84 mm. from the unknown locality, 4·47 mm. from Romsey, 6·45 and 4·75 mm. from the French and 4·76 mm. from the Swedish *loci*. The question naturally presents itself—are the Scilly forms juvenile? We do not think this possible, for, if they are juvenile, the complete absence of large specimens must indicate that the species is an annual*; but (1) Hasay (1881, p. 73) says specifically that this species (as *P. spirorbis*) lives for two years; (2) in the numerous series of

* We obtained 500–600 specimens in all.

this species in the British Museum there are always large specimens present along with small ones from the same locality. In itself dwarfing is not an uncommon phenomenon, and has been recorded as the result of various environmental anomalies (Pelseneer, 1920, pp. 561, 628).

The St. Mary's forms, however, not only differ in size from the other English series and the continental ones examined by us, but they also differ (*a*) in the proportion of the last whorl and (*b*) the mouth. The following table gives the facts:—

| Average diameter (mm.). | % body-whorl width. / Max. width. | % aperture length. / Max. width. |
|---|---|---|
| St. Mary's, 3·316. | 26·3 per cent. | 30·9 per cent. |
| Cleveden, 4·535. | 21·0 ,, | 26·4 ,, |
| Romsey, 4·4. | 24 8 ,, | 26·8 ,, |
| Agen (France), 6·45. | 22 3 ,, | 24·7 ,, |
| Oise (France), 4·74. | 22·4 ,, | 27·2 ,, |
| Suex (Stockholm), 4·76. | 21·0 ,, | 24·1 ,, |

It will be plain that there is an appreciable tendency for small shells to have wider body-whorls and longer apertures than large ones. The number of series is however small and the apparent decrease in the width of body-whorl and aperture-length is irregular. This was further tested by taking two large size-series of Somerset shells, with the following results:—

| | % body-whorl width. / Max. length. | % aperture length. / Max. length. |
|---|---|---|
| Class 1: average length 5·2 mm. | 22·2 | 27·4 |
| Class 2: ,, ,, 3·8 mm. | 22·1 | 28·0 |

We are inclined to believe that this last series gives a more accurate picture of the growth-rate as the number of individuals measured was much larger.

While we cannot speak as yet about the Cornish forms of *leucostoma*, it seems that those from St. Mary's are peculiar in the size of the body-whorl and aperture. As to the small size we reserve judgment. It is almost certainly not due to age, but it is likely to be a modification found elsewhere.

## 4. Ecological.

### a. *The Habitats occupied by the various Species in St. Mary's and Land's End.*

In comparing the species living in our two areas it is desirable to ascertain if they occupy the same kind of habitat in both areas. Habitudinal divergence is just as important as structural divergence in evolution, and we should therefore inquire to what extent the one precedes the other. We do not wish to discuss the classification of Molluscan habitats in this paper, but it is necessary to point out that it is very difficult to make very rigid definitions. In the present paper we have defined nine broad types of habitat

and rejected temporarily all records which do not correspond with one of these main types. The comparison of homologous habitats in St. Mary's and Land's End has likewise been a difficulty, for it is never quite certain if habitats similar in a general way are exactly comparable.

1. *Walls.*

We distinguish two types of wall according to (*a*) the presence or (*b*) the absence of hedge-like growth covering the stone-work. The first type is not very common in St. Mary's, though quite common in Land's End. We therefore compare only type (*b*) in the two areas. The following points are to be noted:—(1) St. Mary's (7 stations) has four species (all slugs) not taken on walls in Land's End, while in the latter (10 stations) eleven species are recorded from walls which do not occur on walls in St. Mary's. (2) Slugs are more common on walls in Scilly than in Land's End. (3) *Cepea nemoralis* and *Hygromia striolata*, which are very well represented on walls in Land's End, do not occur at all in this habitat in St. Mary's. Thus *C. nemoralis* occurred in 6/10 walls in Land's End and in 0/7 in St. Mary's. (4) The most frequent wall association in St. Mary's is *L. cylindracea*+*Hy. nitidula*; in Land's End it is *H. striolata*+ *C. nemoralis*.

2, 3. "*Waste*" *areas; quarries and pits.*

No comparison between the St. Mary's and Land's End habitats are possible, though we obtained a good many records.

4. *Sea cliffs.*

On St. Mary's the cliffs tend to be more uniform in character than in Land's End. They are abrupt, rocky, and less diversified by natural and artificial talus. Classification according to the dominant vegetation seems to be the best method of distinguishing the various kinds of cliff:—

1. Cliffs with *Silene*-mats.

The St. Mary's fauna is an impoverished version of that found in Land's End, the characteristic species being identical in both cases.

2. Cliffs with mats of Thrift.

*Hy. draparnaldi* did not occur in the Land's End stations; nor were *H. virgata* and *V. excentrica* obtained in St. Mary's. The number of stations in the two areas was rather low, so that the absences may not be significant.

Except where there is a mat of Thrift or *Silene* the cliffs in both cases are very poor in snails. Several *loci* in each area were quite barren (*e. g.* Samphire-patches).

5. *Trees.*

In St. Mary's we obtained snails from Elm alone (*v.* above, p. 1106), and the only form recorded is *Balea perversa.* In Land's End this species is found on Elm along with *H. aspersa* and *L. arborum*, *A. ater*, *L. cylindracea*, and *C. bidentata* (which is not found at all in St. Mary's).

6. *Sandy areas.*

This category includes sandhills, dune pasture, and Marram-dunes. Of the more numerous species *H. virgata* is found in all the Land's End dunes and is absent in our St. Mary's stations. Conversely, *H. aspersa* is very common in St. Mary's and rare in Land's End dunes, the figures being large enough to be significant. The common Scilly association is *H. aspersa* + *C. barbara*; that of Land's End is *H. virgata* + *C. barbara.*

7. *Heath.*

There is considerable difficulty in distinguishing the various kinds of heaths from the data at present available.

I. *Erica*-heath with grasses.

The Cornish stations yielded no snails at all. In St. Mary's we obtained *Hy. nitidula* and *cellaria*, *A. ater* and *G. rotundata.*

II. Grass (*Holcus*) heath regenerating after fire.

This habitat is fairly rich in both areas. Land's End yielded seven more species than St. Mary's, the number of stations being three and four respectively.

III. Grass between clumps of *Ulex* (mainly a later stage of 7 II.).

There are not enough stations to allow us to make a suitable comparison.

The outstanding feature of this type of habitat is the poverty of the Land's End heath fauna. Thus in Land's End eight stations yielded 44 specimens (5·5 apiece), while in St. Mary's five stations yielded 125 (25 apiece).

8. *Marshes.*

Various types were examined in each area, but not enough of any one sort to enable us to institute comparison.

9. *Fresh water.*

A difference in the type of stream and enclosed water which we encountered in the two areas renders it possible to make a comparison of the ponds alone. In St. Mary's the Limneas (*peregra* and *truncatula*) are usually mutually exclusive, occurring together only once in six stations. They occur together in

Cornwall and are also found associated in "trickles" in cliff-faces. On the island and mainland alike *truncatula* invades horse-troughs. We have the distinct impression that *Planorbis leucostoma* is more abundant in St. Mary's than in Cornwall.

One of the most interesting points that has impressed itself upon our attention is the possibility that a species living in Land's End and Scilly may not occupy the same habitat in both places. We have indeed a good many records which seem to suggest that several of the species found on St. Mary's do actually occupy different habitats or do not have the same range of habitats as they do in Land's End. The validity of such evidence as a proof of a definite change of habit or behaviour must of course depend on the number of cases available. The occurrence of a species in a different series of habitats could only be regarded as significant if there were many records. At present we do not consider our records sufficiently numerous to enable us to publish any definite instances of this difference in habitat. The only cases of which we are at all confident are :—

| | | | | | |
|---|---|---|---|---|---|
| (1) *H. aspersa*, | found | in $\frac{5}{7}$ | sand-dune | stations | in St. Mary's. |
| | ,, | ,, $\frac{1}{7}$ | ,, | ,, | Land's End. |
| (2) *C. nemoralis* | ,, | ,, $\frac{0}{10}$ | wall | ,, | St. Mary's. |
| | ,, | ,, $\frac{0}{7}$ | ,, | ,, | Land's End. |

### b. *The Incidence of the Species in Granite and Non-Granite Areas.*

Differences in geological formation are usually considered to have very little direct influence in determining the racial differentiation of molluscan species, their distribution and habitat-preference. A few species are "calciphilous" or "calcifugous," though we do not know for certain that it is the presence of lime that is directly responsible for their distribution. The occurrence of thin-shelled forms on granite and basalt soils is of course well known. But again the issue is by no means clear; for many forms living on non-calcareous soils have solid shells (*cf.* Taylor, *l. c.*). In any case, however, it seems a question for which objective data are required so that a summary of what occurs in our two areas may be of service. We have especially to consider what may be the result in St. Mary's of the restriction of the fauna to granite and alluvium, while in Land's End it has the choice of four soils, diabase and slate being additional to granite and drift there. It may be queried whether there is any advantage in comparing the molluscan fauna of the island with that of *all* our Cornish area. We might of course equally well compare an area like Sennen and Land's End (which corresponds with St. Mary's geologically) with the slaty and diabasic area round Penzance. It might very well be argued that, with slow-

moving animals which form localized colonies, the Sennen-Land's End fauna is as much isolated from Penzance as that of St. Mary's. We are indeed fully convinced that isolation in colonies within the same geographical area may be of great importance in evolutionary divergence; but our present concern is with the effects of insular segregation in a particular case.

A few words may be said about the factors involved in the geological differences between the various areas.

1. *Chemical composition of the rocks and soil.*

In general granite is an "acid" rock, the $SiO_2$ index ranging from 65–75 per cent. The amount of $SiO_2$ in various granites from Land's End varies from 69·42 per cent. to 74·54 per cent. The amount of CaO is low, ranging from 1·40 per cent. to ·21 per cent. The chemical composition of the Scilly granites is not given anywhere; but as they are microscopically identical it is not likely that they will differ very much in chemical composition. The *diabase* (greenstone), which is absent from St. Mary's, is "basic," having $SiO_2$ 50·57–59·84 per cent. in Land's End. The CaO is higher than in granite, viz. 3·71–7·47 per cent. The chemical composition of Mylor slate is not available, but according to Merrill (1897, p. 137) the $SiO_2$ is about 60 per cent. in slate, while the CaO is less than 1 per cent.

The action of weathering upon the chemical constituents of these rocks differs according to Merrill (*l. c.* p. 222), the gross amount of material and the proportions of various chemical constituents lost varying considerably, so that the soil derived from these rocks will differ. In general there seems to be a correlation between the acidity or alkalinity of a soil and that of the rock from which it is derived. According to Atkins (1922) there is in general a relation between "acidity" of rock and low pH value for the soil derived therefrom. But it does not follow that an acid rock will necessarily give rise to a soil of low pH value. Apart from local variations in the amount of humic acid and products of vegetable decomposition (ulmic &c. acid, Merrill, *l. c.* p. 189), Atkins (*l. c.* p. 390) points out that *e. g.* wind-borne spray may substantially increase the pH value of an acid humus. In the present case this fact is of importance (*v.* p. 1105). Atkins and Lebour (1923) have clearly shown that different species of snail are susceptible to different pH values, but in St. Mary's it is very probable that spray-borne chlorine may make up for the lack of basic material in the soil which is due to geological formation.

2. *Vegetation.*

Davey (1909) makes no distinction between the flora of the granite massif and the slaty lowlands of W. Cornwall, and we are unable to find any exhaustive comparison of the two. We are not convinced that the difference *e. g.* between slate and granite is of as much importance for plants as that between other

ecological factors. At present it is impossible to say how far the typical siliceous flora (*Ulex galii*, *Juncus effusus*, *Erica cinerea*, *Pteris aquilina*, etc.) (Tansley, 1911, p. 135) is restricted to the granite massif. *Ulex galii* and *Juncus effusus* at any rate both occur on the slate according to our observations.

To judge the effect and importance of geological formation we may propose a number of questions, the answers to which should clear up the main issues:—

(1) *Apart from the different representation of the various species in St. Mary's and Land's End, are there in the total population under consideration any forms with exclusive preference for any particular soil?*

To answer this a statistical comparison was made between the number of times each species occurred on each type of soil. The result is that no case of exclusive preference was found, though several preferences and several avoidances were strongly marked. The most striking cases are:—

| | |
|---|---|
| *L. marimus* ......... | Marked preference for granite. |
| *Hy. nitidula* ......... | Avoids drift *. |
| *A. subfuscus* ......... | Avoids diabase. |
| | Avoids drift. |
| *H. virgata* ........... | Avoids granite and avoids slate. |
| | Marked preference for drift. |
| *H. caperata* ......... | Avoids diabase and avoids slate. |
| | Fairly marked preference for drift. |
| *C. barbara* ........... | High preference for drift. |
| *H. alliaria*........... | Avoids granite, avoids drift. |
| | Marked preference for slate. |
| *A. granulata* ......... | Avoids diabase, avoids slate. |
| *H. striolata* ......... | Avoids granite. |
| *L. umbilicata*......... | Avoids drift. |
| *M. sowerbyi* ......... | Marked preference for granite. |

It seems that as far as occurrence on St. Mary's is concerned the only critical case is *Hy. alliaria*, which in the total number of stations had a high "slate-preference." The result is that we find it very rarely in the St. Mary's records, in fact only once. Apart from this case there is no instance of a snail having any preference to which residence in St. Mary's should prove objectionable on grounds of the soil.

(2) *In the case of the forms which differ structurally in Scilly and Cornwall, are the differences correlated with any differences of occurrence on geological formation?*

* In making this calculation we have joined under the term "drift" all the stations on alluvium, gravel, sand, and "head." The term is not very suitable as it usually has a more limited sense than that employed here. But it is the most appropriate which we can find. In practice nearly all these records are from sandhills. For the time being we do not differentiate between the various elements described as *drift*, e.g. whether "drift" means sandhill or gravel pit. The main contrast in considering *soil* is between granite, slate, and drift.

When the individuals of a species from Land's End differ from those found in St. Mary's we cannot show that such differences are correlated with the occurrence of such forms on different soils.

(3) *Are there any differences in the structure of snails from the granite of Land's End and those from the slate of such an order that they exceed those between the granite of St. Mary's and that of Land's End?*

At present this question cannot be answered as the individual lots from slate and granite are not large enough to be compared. In three cases in which fairly large numbers are available there are no such differences.

(4) *Is any species found on a given soil more frequently in Land's End than in Scilly?*

The question was dealt with as in the case of No. 1. The percentage incidence of the species on the various formations in the two areas was calculated and compared with the actual percentage of such soils in the total number of stations. Slate and drift are treated as "non-granitic." The answer to this question is quite definite. The percentage incidence in the two areas is not the same; for in one or two cases a form may have a different preference to granite in St. Mary's and Land's End, e.g. *Hy. draparnaldi* and *A. agrestis*; or, as in the case of *L. umbilicata*, granite may be preferred in St. Mary's and non-granitic soil in Land's End. There are actually thirteen species which show such differences in preference.

## 5. The Past History of the Scilly Isles.

It would be of great interest if we could ascertain how long the Scilly Isles have been isolated from the Cornish mainland by the present channel, as we might with certain qualifications obtain by this means a measure of information on the local rate of evolution. This subject, however, is very obscure, and we do not feel confident that any definite date can be yet assigned to the subsidence which separated Scilly from Cornwall. There are, however, certain indications (1) that the present fauna is post-glacial, and (2) that the subsidence may be of Neolithic date. As the matter is still very uncertain we only present the evidence in an abbreviated form.

(1) It is impossible to make use of the "Lyonnesse" tradition of extensive submergence west of Land's End in historical times. Though legend may be an important source of historical evidence, in the present case the story of the Lyonnesse subsidence is neither specific enough nor consistent (*cf.* Ussher, 1879). The attempts to identify the Scillies with the various islands referred to by the ancient geographers (Diodorus Siculus, Strabo, etc.) are not very successful. But we cannot ignore the fact that somewhere about the beginning of the Christian Era there was a group of islands approximately in the position now

occupied by the Scillies. The fact that tin was said to be obtained from these islands, though there is scarcely a trace now, is not very important as the Cassiterides as a trading area may have included the tin-bearing coastal parts of the mainland (*cf.* Carne, 1822, p. 354). One is therefore inclined to believe that the Lyonnesse legends are more likely to relate to small local subsidences of the Cornish coast for which definite evidence is available, than to the severance of the Scillies from the mainland, which probably took place long before the first century B.C.

(2) Argument from the depth of a channel to its age is a very insecure method unless accompanied by some knowledge of the local conditions (*e. g.* effects of tidal scour or sedimentation). The Scilly channel has an average depth of about 36 fathoms, and is therefore much deeper than the Straits of Dover, and about equal in depth to the Pentland Firth. If this depth really represents the depth of the actual subsidence, and has not been modified either by subsequent excavation or by the filling-in of an originally deeper channel by deposition, we must look for evidence of a land movement of some thirty fathoms (180 feet). The Scilly channel is not one in which much deepening would occur, as it is not a narrow strait. Dr. G. H. Fowler informs us that the evidence points in most places round these coasts to fluctuations between erosion and deposition. We therefore tend to believe that the Scilly channel may represent the actual depth of subsidence.

Before we consider the vertical movements of the coast-line in this area," it is as well to point out that the evidence of the glacial drift on Scilly is negative. The occurrence of glacial deposits with chalk flints, greensand, chert, and sandstone débris recorded in the Geological Survey Memoir (Barrow, 1906, pp. 21–23) is stated by Barrow (*l. c.* p. 27) to be due to transport by floe-ice. If this is true it does not follow that the islands were separated from the mainland when this deposit was laid down, for a deposit similar to part of the Scilly drift is found on the coast of Brittany (Barrow, *l. c.*). There is no trace of the action of land-ice in this area (Barrow, *l. c.*; Reid and Flett, 1907), so that we are deprived of evidence from that source.

There are two main epochs of submergence to which we may appeal for the separation of the islands :—that of Pliocene times ((Barrow, *l. c.* p. 15) and the general evidence from Cornwall (*cf.* Dewey, 1909; Reid and Flett, *l. c.* p. 71)), and a subsidence of a comparatively recent date (? Neolithic) the effects of which are also seen in S. Ireland, S. Wales, and Cornwall and in other parts of the British Isles. The ascertained (but not of course the actual depth) of the latter is about 40 feet (Barrow, *l. c.* p. 33), though Mr. H. Dewey informs us that evidence of a deeper submergence is found in deposits near Helston giving about 100 feet. This might give us some 16 fathoms, or half our required depth. As for the Pliocene submergence, all we know is that the Cornish land surface was originally very much lower

and that there has been an elevation of some 430 feet at least. We do not actually know if this elevation ever brought the islands into contact with the mainland.

We are therefore unable to speak with any certainty as to the date of separation, though before the Neolithic subsidence of 16 fathoms the distance of the channel would be considerably reduced by the fact that the Seven Stones and other shoals would probably be dry land. It is very pertinent, however, to point out that if Barrow's views (*l. c.*) as to the action of the floe-ice in depositing the "Head" is correct, then the islands must in Glacial times have been scoured by the masses of ice that swept over them, and in all likelihood the mollusc population would be very much diminished, even if it escaped total destruction. If the Scillies were subject in glacial times to the same conditions as hold today in Spitzbergen or South Georgia, it is almost certain that the major part of the old land and freshwater population of mollusca would have been destroyed.

## 6. Disturbance of the Fauna by Human Occupation.

The Scilly Isles have been occupied by man since prehistoric times to judge by the occurrence on them of tumuli and kistvaens probably of Bronze Age. In the early Middle Ages Tresco Abbey was of some importance and was probably in constant communication with the mainland. Later the islands were of some importance as a point of naval strategy. It is therefore possible that chance importation might bring in mainland snails, though we think that, unless fodder or vegetables were imported on a large scale. this is unlikely. The introduction of exotic or continental plants into the gardens of Tresco has not so far led to the finding of any exotic snails, as it has of insects (*e.g.* the New Zealand scale-insect, *Eriococcus hoheriæ*). Mr. G. W. Gibson tells us that newly-lifted bulbs are brought over from the mainland, and we are informed by Mr. J. C. Fryer that all the insect pests of the mainland have been introduced. No evidence of the actual introduction of snails in recent years is available; but such introduction is possible. However, the horticultural trade is comparatively recent, dating to between 1864–1893 (Somerville, 1893, p. 119), so that this source of contamination is not likely to have had much effect. In any case it is not likely to have had any effect whatever on the majority of species which live away from gardens. We can offer then no evidence that introduction of snails has not occurred; but it seems to us very improbable that the ordinary accidents would bring in enough immigrants to alter the population substantially (except possibly in the special case of certain slugs). Certain of the insular forms described above show differences of more or less undoubted significance. The common *H. aspersa* is among these, some of the widely distributed forms of which are absent. The common and widely distributed *Cepæa hortensis* is absent, as well as two

garden species of *Testacella* and *Arion circumscriptus*, all of which, if artificial introduction were in operation, should in normal expectation have turned up on St. Mary's.

## 7. Summary and Conclusions.

(1) A preliminary survey of the land and freshwater mollusca of the island of St. Mary's (Scilly Isles) and the Land's End district west of Lelant and Marazion has been made, and the structural divergence between the insular and mainland fauna is recorded as far as it appears significant.

(2) The habitats occupied by these forms and the incidence of the latter on the various geological formations of this district are recorded and analysed.

(3) A preliminary estimate is made of the differences between St. Mary's and Land's End in climate, soil, flora and fauna. It is concluded that as far as the mollusca are concerned the following characteristics of St. Mary's are important:—

(1) The dry, warm and equable climate;
(2) the lack of trees;
(3) the probable occurrence of spray-borne chlorine over the whole surface of the island;
(4) the lack of carnivorous beetles and small rodents.

We believe that (3) more or less may counterbalance the low pH concentration of the soil resulting from the granite formation.

(4) The species of snails are only slightly less numerous in St. Mary's than they are in Land's End, though they are only half as numerous as the total number recorded from West Cornwall.

(5) Structural differences between the insular and mainland snails are noticed in twelve cases, and, as far as we can say at present, very few of these peculiarities occur elsewhere in the British Isles or Europe. The evolutionary significance of these differences is obscure at present and steps are being taken to procure more material for their statistical treatment. But in most, if not all, cases the differences are neither of specific nor even of varietal rank, but seem to be of the order usually found between isolated colonies in the same area.

(6) These structural differences cannot at present be related to any particular difference in habitat or environment. Differences of association and habitat, however, are obviously being formed in the island.

(7) The fauna is probably post-glacial in age, as we believe that the Pleistocene fauna was swept away by floe-ice grounding on the Scilly area, or by the general glacial conditions.

(8) The islands were probably separated from the mainland in Neolithic times, but this point is uncertain. Since that date we believe that mainland forms may have been introduced from Cornwall; but we do not think that such introduction would have a marked effect on the Mollusc fauna.

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# 58. Observations on the Mating Habits of some Web-spinning Spiders. By G. H. Locket, B.A., with some corroborative Notes by W. S. Bristowe, B.A.*

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(Text-figures 1–4.)

The following observations are concerned chiefly with the mating habits of various spiders, and particularly with pre-coition activities and courtship. I have, however, added other notes about the care of the young and so on in some cases.

Mr. W. S. Bristowe, to whom I showed this paper, has very kindly supplied me with some notes of his own on some of the species I have studied. His observations were made in 1920 and 1921, and appear now for the first time. Naturally, I am very grateful to him for allowing me to include his independent observations, which must enhance the value of the paper.

The study of the mating of spiders has yielded results which are of considerable biological importance, and which give us information about the mentality of these animals not easily obtained by the study of their ordinary every-day activities.

In spiders possessed of a sense of sight, mating is often preceded by a display on the part of the male, the best examples being found among the Attidæ, studied by the Peckhams (1890). The Lycosidæ were studied by Montgomery (1903, 1908, 1909, and 1910), and a paper has just been published by Mr. W. S. Bristowe and myself, where Mr. Bristowe has indicated the lines along which these display movements probably evolved.

The web-spinners so far as we know possess no power of distinct vision (beyond a very short distance), and correspondingly no display in the ordinary sense exists. However, as the Peckhams pointed out (1890), in such spiders the male communicates with the female by means of vibrations in the threads†, and a "tactile display" is at all events a possibility. A number of points arise from my observations which will be discussed when the actual facts have been related.

The species studied are very different, but are considered together for purposes of comparison. They include *Theridion sisyphium*, *T. lineatum*, *T. denticulatum*, *Steatoda bipunctata*, *Linyphia clathrata*, *L. triangularis*, *L. leprosa*, *Zilla x-notata*, *Epeira cucurbitina*, *Dictyna latens*, *D. uncinata*, *Amaurobius similis*, and *Agelena labyrinthica*.

## Theridion sisyphium (Clerck).

This spider is exceedingly common on bushes and hedgerows during the summer months. It is mature in early June, when

* Communicated by Prof. Julian Huxley, F.Z.S.

† *Vide* also W. S. Bristowe (*loc. cit.*).

mating takes place. I have observed the mating, with specimens kept in captivity in a triangular glass case, on June 12th, 14th, and 15th (1925).

On introducing the male to the female's web both spiders at once showed evident signs of excitement. The male wandered about making movements with his palps, his abdomen pulsating, while the female shook the web with quick motions of the legs (which she never does under normal circumstances), her abdomen also vibrating. These shaking movements then gave place to curious rhythmic movements, and the male, apparently guided by them, gradually made his way to the female, and an interplay of legs ensued. He then turned round and walked away, but soon came back. (On two occasions during his wanderings he stretched out all his legs, exactly as when casting a skin, and trembled violently.) The same interplay of legs now took place, whereupon the male felt the female's sternum and the underside of her abdomen (now uppermost, since both spiders were inverted in the web) rapidly with both palps. He apparently had difficulty in finding her epigynum, probably on account of her movements, which were continuous, and he kept pushing his palp along the underside of her abdomen. At last his left palp was applied; then followed an interplay of legs, and the right palp was applied. During each application the female became rigid and immobile, her palps and front legs extended stiffly (text-fig. 1). The male now retired to a distance of about 1 inch, and proceeded to make a tiny bridge of several strands of silk across two strands of the web. He rubbed the underside of his abdomen against this, depositing a minute white opaque drop of sperm, which could be seen distinctly under a lens, and to which the palps were applied alternately with a quivering movement. All this time the female was making jerking or rhythmic movements. The male now approached the female and mating followed exactly as before. The following is a summary of the mating for as long as I watched it:—

Male approached; left palp applied 7 secs., right for 5 secs. Retired and took up sperm in palps.

Male approached again; palps applied 6 and 12 secs. Retired and took up sperm (at another place).

Male approached again; right palp only (8½ secs.).

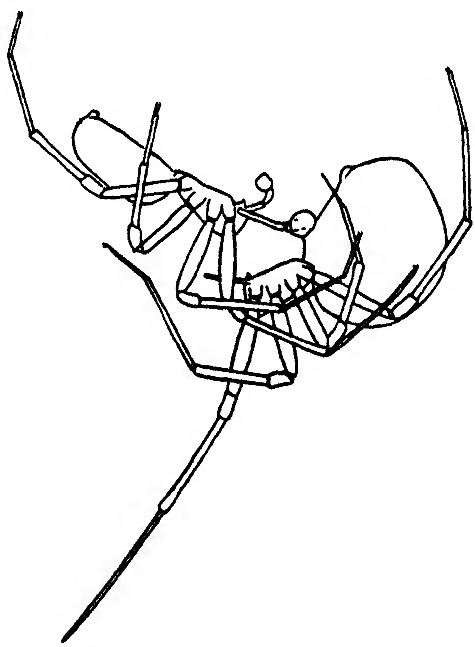
The whole proceeding was then repeated six times in one hour forty minutes, when I ceased watching. Every application of the palp was accompanied by the usual inflation of the hæmatodocha. On no occasion did the male apply either palp more than once before recharging it with sperm, which is most unusual.

An interesting point is the part played by the female in the courtship (if we may thus describe the pre-nuptial movements). It is quite as important as that of the male, since he could not find her easily unless she made rhythmic movements. If a male is put into a female's empty web, he is excited (as shown by his

abdomen pulsating) and searches about in all directions for her. Also her movements probably have a stimulating effect while he is recharging his palpal organs.

The mating appears (except for relative positions during copulation) to be very similar to that of *Theridion tepidariorum*, observed by Montgomery (1903), and resembles that of *Theridion denticulatum* (Walck.), observed by Berland (1914), except that in the latter species sperm induction appears to be much less frequent.

Text-figure 1.



*Theridion sisyphium*. Relative positions of ♂ and ♀ during copulation. (Limbs on near side only are drawn.)

The first batch of eggs of *Theridion sisyphium* are laid about the middle of June (*e. g.* 15th and 17th), and other batches often follow later. The mother encloses the eggs in a greenish cocoon, which she guards under a kind of tent surrounded with bits of leaves or dry bodies of flies etc. She is very much attached to her eggs and, if they are removed, searches with her palps all over the tent for them. If they are returned within about 72 hours, she will seize them and retain them. If a longer period has elapsed since their removal, she is reluctant to take them

back and very soon rejects them. Experiments of a similar nature on various Lycosidæ and *Theridion globosum* (Hentz) (1887) led the Peckhams to the conclusion that the spiders remembered their cocoons up to the time at which they refused to accept them. I think there is no doubt whatever that this is not a case of associative memory at all. The spider at certain seasons reacts directly to the feel or smell * of its cocoon, and the power to react will persist for a time after its removal. When new eggs begin to develop (which presumably happens when the 72 hours have elapsed, since spiders of this species which had refused their cocoons very soon laid more eggs), the reaction to a cocoon will be in abeyance until a new one is formed.

The first batch of eggs hatches about the first week in July, and then begins a very curious family life of a kind very rare among spiders. It was noted by Blackwall (1864) and by Pickard-Cambridge (1879) that the young lived with their mother until they were quite large; indeed, the fact is well known to arachnologists. One or two notes I made in 1923 and last year (1925) may, however, throw a little more light on the question. When a fly becomes entangled in the web the mother runs out and secures it in the usual manner, *i. e.* throws viscid lines onto it with her back legs until she can approach, then bites it, usually in a projecting limb; the poison is powerful and the fly is motionless, as a rule, within five minutes. The young spiders (even though just out of the cocoon) then find their way to the fly; how I cannot say, but guided probably by the movements made during its capture †. The mother begins to move over the body and bites it in a number of places (this she does not do if she has no young, but restricts herself to two or three spots). The young were watched with a horizontal low-power microscope. They crawled over the surface of the fly, feeling it with their palps, and stopping to apply their mouths to soft spots such as joints and particularly to holes made by the mother; rhythmic motions, due to sucking, would then follow. On several occasions this year I found two or three young spiders collected round the mother when she was not feeding, and on examining them with a microscope found that their mouths were applied to hers. Presumably then she was feeding them. I have never heard of another instance of this habit among spiders.

The growth of the family is most interesting to watch. The method of attack peculiar to Theridiidæ is used right from the beginning. Even the very young spiderlings are to be seen busily throwing their tiny viscid lines onto the struggling fly that their mother is securing. Later in life their assistance may

* With Lycosidæ (which will take paper pellets, snail shells, etc., instead of their cocoons) smell cannot be operative, but the feel of a round object of about the right size will produce the reaction. Theridiidæ (which live in more intimate contact with their cocoons) are more particular as to their texture, and refuse substitutes.

† In some cases the fly is taken back to the nest, but often not.

be of real value to her. The members of one family, whose mother I removed when they were large enough, continued to live together. They were often quarrelsome while attacking the same fly, and threw viscid lines at each other long after their prey was motionless. However, they were quite immune to one another's attacks. Their legs will not stick to the lines, provided they are passed through the jaws from time to time (which Hingston (1923) showed was the case with *Nephila maculata*), and a particular spider appears to fear his brothers' viscid lines no more than his own. This seems to me a very important fact, because a *Theridion* never bites until his victim is partially incapacitated with the viscid lines. Thus spiders so defended one against the other can live together and gain the advantages of their mother's web. Moreover, we may have here a basis for what appear to be truly social habits in species such as *T. eximium* (Keyserling), observed by Simon (1892). Blackwall mentions a family life as occurring in *T. lineatum* and *T. riparium* (Blackw.), and Bristowe (1924) records it in *T. pictum*; so it is fairly frequently found among Theridiidæ. For purposes of comparison I kept some young of *Epeira cucurbitina* together in one vessel (they soon disperse in nature) and fed them on gnats and small flies, which were set upon, killed, and eaten by several of the young spiders together. They frequently attacked and sometimes killed each other, but common life of a sort was possible. The fact that these spiders usually bite straight away without trying to enwrap their prey, however, precludes the possibility of continued family life. The irregular nature of the webs of Theridiidæ may also account for the persistence of the habit with them; Mr. W. S. Bristowe (1924), in speaking of contiguous webs of *Epeira gregalis* and *Pholcus phalangioides*, suggests that an advantage is gained in increased strength and economy of tie-lines.

THERIDION LINEATUM (Blackwall) (=*Phyllonethis lineatum* (Thorell)).

This species is found commonly on low-growing plants in hedgerows, and reaches maturity about the middle of July. Its movements are curiously slow compared with those of other Theridiidæ, but it spins and captures its prey in the same way.

*Mating.*—On August 2nd a male was introduced into a female's web. He began walking about in a curious jerky manner, his abdomen first pulsating and then vibrating very rapidly. He approached the female, who made two or three jerks on the web; he circled round, approached again, caressed her with his front legs, then approached closer and applied his palps alternately. The relative positions of the male and female were now the same as in *Theridion sisyphium*.

Applications:—Left palp 10 times, right palp 10 times. Average duration 10 seconds.

The female then moved suddenly and the male dropped, but approached her exactly as before and applied his palps.

Applications:—Right palp 40 times, left palp 47 times. (Applications not always with alternate palps; they at first lasted about 12 seconds, but mostly for 5–7 seconds.)

Total time for mating 12–15 minutes.

The female now suddenly started to attack the male by throwing viscid lines onto him, and he was removed. He had already mated with another female who had treated him in exactly the same way, and he would certainly have perished had I not removed him.

Theridion denticulatum (Walck.).

This species is common in windows of houses. The mating was described by Berland (1914), and my own observations entirely agree with his.

The first eggs are laid in May (25th and 27th) and are enclosed in a greyish cocoon. They hatch in just over a fortnight. During this time the mother remains with them and builds a sheet which protects her and them. She takes no food until the eggs are hatched, when she often leaves them. The young soon disperse, and there is no kind of family life. One female I found turning over her cocoons of eggs (which were not fertile) and solemnly biting each egg with her fangs. She felt the cocoon all over, and turned it repeatedly to be sure of missing none. I do not know why she was doing this, unless it is that the mother has to release the young from the cocoon, and therefore remains with them until they are hatched. This would account for the protecting sheet, which would prevent her getting separated in any way from the cocoon. I have found dead young in a cocoon taken some time previously from a female of *Theridion sisyphium*, so that it seems likely that mothers do have to liberate the young. Emerton (1883) observed a *Theridion* gnawing her cocoon shortly before the young emerged.

The following is Mr. Bristowe's account of the mating of this species:—

"My observations on *Theridion denticulatum* also agree, so far as they go, with Berland's. I placed a male in the web of a female with which he had copulated earlier on the same day (April 25th, 1920). He advanced, giving twitches of his abdomen at intervals, until he was quite close to her, and then she herself crept beneath him (they were both in an inverted position). The insertion of a palp consisted of little more than a lunge at the female vulva accompanied by one or two rapid vibrations of the abdomen, during which time the hæmatodocha rapidly swelled out and collapsed. Each palp was inserted several times before it was changed for the other."

STEATODA BIPUNCTATA (Linn.).

This spider spins an irregular snare which is commonly found in corners of outhouses.

*Mating.*—The spiders mate after dark. On putting a male into a female's web, he walked about with a peculiar gait while she made a series of sharp plucking movements on the web. Whenever they encountered each other there ensued what can only be described as a wrestling match; but there was no attempt by the female to attack the male, which she would have done by throwing viscid threads onto him. The actions of the male now became a little more definite; he walked backwards and forwards, spinning over a small area, the female making plucking movements and sometimes approaching him, when an interplay of legs, palps, and even jaws would again take place. After about a quarter of an hour of this spinning, the *female* approached and there was the usual interplay of legs; the male then extended his palp and applied it rapidly to her epigynum. The movement was most curious, and reminded one irresistibly of a fencer making an attack. He repeated this with the same palp five times, put it through his cheliceræ, did the same thing another five times, and so on. Whenever he stopped to put his palps through his jaws the female appeared very excited, making plucking movements continuously; but she was quite motionless when he was actually applying his palp, which was only in contact with the epigynum for about half a second at each application.

I do not think this constituted the whole mating, since there was no inflation of the male's hæmatodocha (*cf.* Emerton on *Steatoda borealis* (1882), where the male's palp was applied for one hour). I am therefore very grateful for the following details of Mr. Bristowe's observation (although he also makes no mention of the swelling of the hæmatodocha):—

"My observations on *Steatoda* agree fairly closely with yours, especially as to the spinning of web by the male in a fairly methodical way in one small portion of the snare. I observed the courtship and copulation on March 11th, 1921, the latter taking place in the afternoon (*i. e.* in daylight). In my case the male had to coax the female out from her retreat. This he did by repeatedly entering her tubular retreat, vibrating his legs slightly as he did so, and then coming outside again. Eventually she did come a little way out, plucking the web with her legs as she came. He approached with one palp raised and the other lowered, and then, when in reach, made a violent lunge with the former at the female's epigynum. These lunges were repeated every three or four seconds for a quarter of an hour, the palpi occasionally being changed. At the end of this time the male left her and descended an inch or two lower down the web. The female followed him, plucking the web as she advanced with her front legs, and presently he returned to her, and further applications of the palpi ensued—this time for just over an hour. After copulation the male remained in an upper corner of the web for half an hour and then left it."

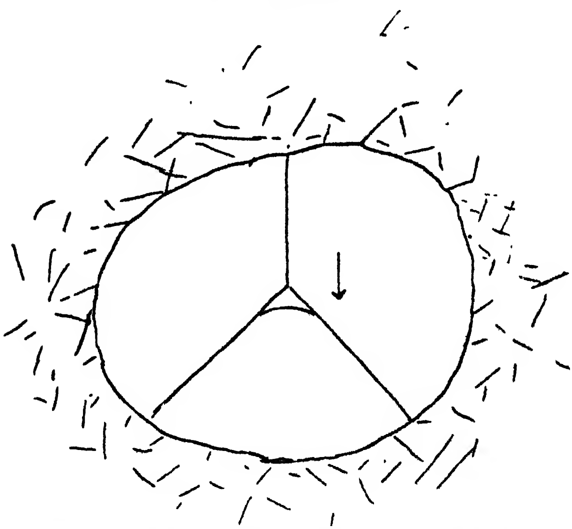
The female I kept (which was mature when captured) laid two batches of eggs before this mating, and both were fertile; consequently one mating is sufficient to fertilise two batches of eggs at least. The male and female lived together after mating, the male sometimes eating flies which the female had left. Probably the male would normally wander, which was not possible for him while under observation.

LINYPHIA CLATHRATA (Sund.).

This species spins a sheet-web among low-growing plants. The following is an account of the mating, which I watched on May 26th (1925):—

I found a male making a hole in a female's web (which was among some plants in a hedge) and enlarging it by walking round, biting away the sheet. When the diameter of the hole

Text-figure 2.



*Linyphia clathrata*. Silk bridge and platform constructed by ♂ for sperm-induction.

was about half an inch, he drew threads across it in the shape of a Y with a little platform of silk in the fork (text-fig. 2). He got *above* this platform (normally, of course, these spiders run on the under surface of the sheet), facing in the direction of the arrow, and moved himself backwards and forwards for one and a half to two minutes, the underside of his abdomen being against the platform. He then got *below* (still facing in the direction of the arrow) and put his palps round the platform so that they sucked up the sperm, deposited there, from above. The palps were applied rapidly and alternately a

number of times. The male then started wandering about the web; the female came in his direction and mating started, but was interrupted almost at once, and the male once more charged his palps, and again the female approached him. The female when they finally separated was obviously excited, and walked about palping the web, her abdomen pulsating. She ran around the periphery of the web while the male tended to follow her more slowly along the inside. He soon returned, however, to the hole he had made, and, by drawing threads across it repeatedly, closed it up completely! He had been leaving a few threads on the web in his wanderings, but this mending had the appearance of a deliberate act.

Montgomery (1903) observed a similar thing in *Theridion tepidariorum*, and the explanation is probably quite simple. The male, although he spins no proper web when mature, is yet susceptible to imperfections in the female's web, and the hole reacts on him as of old and causes him to close it up. The male now continued to pursue the female a little, but soon climbed up a dock leaf and left the web.

*Details of Mating.*—During the second sperm induction there were 15 applications of each palp to the sperm in $1\frac{1}{2}$ minutes.

*Copulation.*—Relative positions as in *Theridion sisyphium* :—

22 applications of right palp.
23 applications of left palp.
Applications were alternate and lasted 6–13 seconds.

The whole observation lasted about three quarters of an hour.

Mr. Bristowe's account is as follows:—

"On March 23rd, 1921, I watched a male *Linyphia clathrata* courting a female for some considerable time, but copulation did not take place while I was there. In this instance the male courtship appears to have been more pronounced than was the case in the one you describe above. I placed the male in some outlying strands of a female's web, and after carefully feeling it with his palps he advanced and climbed onto the upper surface. He walked about until he found her, and then went to the edge and returned to the underside of the web. After a brief pause he advanced, gently shaking the web; she fled; again he paused and then gently touched the web, first with his palps, then his legs; these actions became more rapid, and very slowly he began to advance with quivering abdomen and palpi. Performing these motions he circled round the female, who remained motionless in the centre of the web, anchoring a thread he was trailing every few steps he took. After he had performed two circles round the female he stopped, and then a new set of motions were noticed. He stretched his front legs out in front of him and alternately bent them inwards, the tips of the legs remaining fixed to the web; then, letting go with his front legs, he began to rock up and down in the web, at first gently and then more rapidly; finally, with some twitches of the abdomen

and some movements of the palpi, he came to a standstill. With short pauses in between each, these rocking motions were repeated over and over again."

LINYPHIA TRIANGULARIS (Clerck).

This spider is exceedingly common on bushes and in grass, and is mature in the first weeks of August. The falces of the male are curiously long and conspicuous.

*Mating.*—The male was put into a female's web (in a glass case). She approached him, and he began to walk about on the web, his abdomen pulsating. From time to time he moved his palps along the front of his falces and rubbed the falces all over the surface of the palpal organ. He approached the female, several times touching her with his front legs. She made no objection and showed no hostility towards him. Finally the male approached again, and after feeling her sternum with the back of his palps began to apply them alternately to her epigynum. During this process the whole palp and palpal organ are twisted so that the style and its sheath, which points inwards when at rest, in copulation tends to point outwards. The whole organ is completely removed from its normal position, the inflation of the hæmatodocha being very large. When the palp is removed the twisting movement is reversed and a further spiral movement of the style can be seen taking place; a small white process which is left exposed in the immediate neighbourhood of the style is rubbed with the falces until it disappears.

This passing of the palps by the male through the chelicerae occurs during mating in all the spiders I have watched. In this case obviously the organ has to be carefully rearranged after each application, and it is possible also that the style must be lubricated to some extent by fluid from the mouth.

A male on being put into the empty (imperfect) web of another *male* became slightly excited (as shown by pulsations of the abdomen), but he was very much more excited when placed in the empty web of a female. It is probable that smell stimulates him, and in that case it must be left on the female's threads. It has been shown (Bristowe and Locket, 1926) that among certain of the Lycosidæ the male is stimulated by the smell of the female and also by that of other males; and here we have, I believe, another example, although in this case one cannot remove the possibility of a tactile stimulus from the thread itself.

LINYPHIA LEPROSA (Ohlert).

The mating of this very common species appears to resemble those of the other Linyphiidæ observed. The male approached the female and touched her with his front two pairs of legs, which trembled violently. He then retired and began some spinning operations in the tube (where the female's web was constructed), possibly for purposes of sperm-induction, returning

frequently to the female, who appeared excited also. Part of her epigynum, which is large and conspicuous in this species, was extended in a curious manner during the male's advances, while after mating it was found to be in its normal position again. (I had observed the same thing to a less marked extent in *Epeira cucurbitina* (*v.* p. 1136)). This is interesting as being concrete proof of the stimulating effect of the male's advances on the female.

The whole mating was not watched, but it lasted several hours; the following morning the female was found eating the male, whereas she had shown not the slightest sign of hostility before mating.

Zilla x-notata (Clerck).

The mating of this extremely common spider presents some points of interest. It can often be watched during the evenings in August with specimens that build their webs outside (or inside!) windows. The male climbs to the centre of the female's web and usually seizes the line communicating with the female's hiding place with his four front legs. With his back legs he seizes one of the adjacent radii at the centre and starts a series of jerking and plucking movements on the communicating line, using himself as a sort of spring at the angle of the radii. If the female does not respond he then usually climbs to her retreat, but returns again after an interplay of legs. Sometimes he stops and rubs two adjacent legs together (observed among other spiders, particularly Lycosidæ). Eventually the female comes out, also making plucking movements, and, after a short interplay of legs, the male begins making thrusts at her epigynum (cf. *Steatoda bipunctata*); the palps are then applied alternately. Applications last from 25 to 70 seconds, the female remaining quite rigid with the front legs extended out sideways.

If the male does not encounter the female until he has entered her retreat, he turns round, retires, and approaches again until he meets her *outside* (*cf.* Bristowe (p. 1131) on *Steatoda bipunctata*).

A male on being put into a female's empty web started his movements as usual, and, there being no response, ascended to the female's empty retreat and gradually entered.

The mating of *Zilla calophylla* (probably = *Zilla atrica* (Koch)) was observed by MacCook (1890), but he does not state whether the female in his bottle had constructed a snare. Here again the female "excited her spouse to approach her" by movements of her feet.

The following is Mr. Bristowe's account of the mating:—

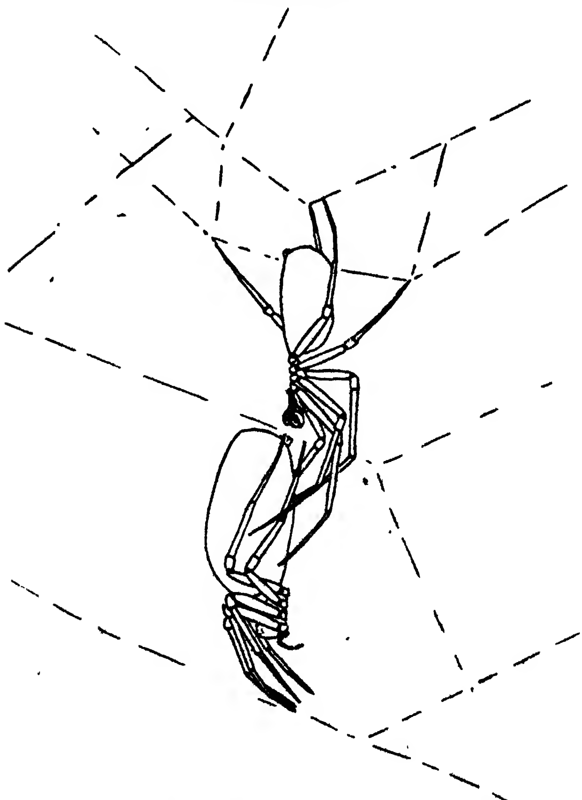
"I have twice seen the courtship and copulation of *Zilla x-notata* (at the beginning of October 1920). In each case the male enticed the female out from her tubular retreat, in one case almost immediately by tweaking the web, in the other only after considerable delay. On first entering the web he tweaked it several times without any result; then he danced up and down on

one of the lines by alternately pulling it taut and letting it go, and finally he succeeded in luring her out into the open by climbing to the entrance of her retreat and rapidly plucking the strands with his legs. After shaking the web and pulling at the lines once or twice, as though making certain of his identity, the female hung down motionless and awaited his approach. The palps were alternatelv inserted for about a minute at a time."

EPEIRA CUCURBITINA (Clerck).

This beautiful apple-green species is mature at the end of May or beginning of June.

Text-figure 3.



*Epeira cucurbitina.* Positions immediately before copulation, showing ♀ rigid and with limbs contracted.

*Mating.*—A female had constructed a web in a triangular glass case and was well fed. A male was introduced who climbed

to some threads connected to the web a little above it and spun more threads there. He then started a series of jerking movements, to which the female responded from time to time by making jerkings of a somewhat similar nature, though often more violent. The male (head downwards) continued to make movements, which comprised a sort of continuous dance, for about a quarter of an hour, when he approached the female with outstretched trembling front legs. She gave a series of powerful jerks, whereat he retired; both spiders continued their jerkings. Then the female *came out to the male*, and, after some rapid jerking movements, threw herself just below him in a crouched and rigid position, exactly as when "feigning death" (text-fig. 3). She remained thus for about a second, during which time the male reached down and made three applications of the palps so rapidly that I failed to record the precise relative positions of the spiders. Whether this was the whole mating or not I cannot say; the female laid six batches of fertile eggs during the summer, but she was mature when captured and may have mated before.

The mating of *Epeira cucurbitina* appears to resemble that of other Epeiridæ, such as *Epeira apoclisa*, observed by Walckenaer (1837), and that of *Epeira marmorea*, *Acrosoma gracile* *, *Epeira labyrinthea*, observed by Montgomery (1903). In the latter case the female's legs during copulation were "loosely flexed" as in *Theridion tepidariorum*, but in the other three species the female's legs were "flexed close." Short quick applications of the palps are the rule, as opposed to those of *Zilla x-notata*, which are prolonged.

Dictyna latens (Fabr.).

The male and female of this species (as in *D. arundinacea* and *D. uncinata*) live together in one nest. I have kept them thus from the middle of June to August 15th (when the female died); but it is unlikely that they live together for so long in the ordinary way. They both spin the web peculiar to their family, and will attack the same fly (I have seen males overcome flies alone) and feed together. I once saw a hungry female drive a male away from a fly until she was satisfied, and one male was found dead and eaten in one of my cases, but if food is plentiful they appear to live happily together. Several cocoons are constructed (*e. g.* six or seven), each containing about six eggs; it is possible that the female has to be fertilized for each one or two, but I have not yet determined this. The young soon disperse on hatching and are not tended or fed by the parents.

*Mating* takes place frequently in June. There are practically no preliminaries; the male comes right up to the female and gets underneath her and applies his palps one at a time. The relative positions are approximately as in *Theridion sisyphium*, except that the spiders are not inverted (*cf.* Montgomery's figure (1903))

* The relative positions during copulation are different in this species.

and the male's right palp is applied to the right of the female's epigynum. During the swelling of the hæmatodocha the palp is turned over so that the outside of it comes against the female's epigynum. A rapid play of legs by the male took place as he was changing over to apply the other palp. There were 4 and 3 applications of the right and left palp respectively; jerking movements occurred occasionally and pulsations of the male's abdomen. The whole process took about a quarter of an hour.

The male when he recharged his palps spun a minute sheet of silk, the edge towards which he faced being curved inwards. A drop of sperm was deposited on the sheet, and the palps appeared to be applied to the underside of the sheet. However, with *D. uncinata* they seemed to be applied to the upper surface (and Montgomery (1903) has observed this in *D. volupis*), but owing to the fineness of the sheet it was very difficult to make certain. The male showed considerable excitement during the sperm-induction, his palps and abdomen working continuously.

The following are Mr. Bristowe's observations on this species and on *Dictyna arundinacea*:—

"Although I agree that courtship is not very marked in *Dictyna latens*, my observations show that there are some preliminaries, for the male has been seen on several occasions walking about in a female's web with vibrating legs and occasional twitches of the abdomen. The female appears to recognize these as the signals of a suitor, for, sometimes without turning to meet him, she will respond with similar vibrations. The male does not seem to be at all frightened of the female, but advances and tickles her with his vibrating legs: this presumably has a stimulating effect upon her, and it is a very common occurrence in the courtship of spiders in general."

"*Dictyna arundinacea.*—On being placed in the web of a female, a male advanced towards her with vibrating front legs, with which he proceeded to tickle her. She made no attempt either to escape or to attack, but responded by waving her legs in similar fashion, and then proceeded to turn her back on him. He continued to tickle her with vibrating legs, and, as before, she responded for a time and then turned away from him. This happened three times, and then he began bustling about the web, still with his legs vibrating excitedly, biting away threads which came in his way and weaving fresh ones in the manufacture of what appeared to be a rough canopy. When, in the course of his wanderings, he came across the female, vibratory salutations were exchanged. After he had completed his weavings the female approached and appeared to inspect his handiwork, and he, with vibrating legs and an occasional twitch of the abdomen, gently squeezed himself under her and inserted one of his palps. The above observations were made in the early summer of 1920, but whether the "canopy" was built for sperm transference or whether it was an accidental chance that copulation took place beneath it further experience alone can prove."

DICTYNA UNCINATA (West).

Copulation was observed on June 11th and on July 13th (when young were hatched). I found a female with eggs on May 27th, so that the mating period lasts a considerable time. The common life is the same as in *D. latens*, the male and female often remaining motionless for long periods, their legs in contact. (Males and females of *D. arundinacea* do likewise.) Several cocoons were constructed each containing 6 to 8 eggs.

AMAUROBIUS SIMILIS (Blackw.).

The males of this species are found wandering towards the end of August and September in large numbers in outhouses, and they may live for four or five months (they are still numerous in January and February *).

The courtship is most marked. A male on arriving at the outskirts of a female's web starts a series of synchronized plucking movements with both palps. As he advances he attaches a thread to the web, and his abdomen, pulsating with the usual excitement, causes a considerable area of the web to move also, which movement must be communicated to the female. I have watched specimens in captivity. The female had woven her snare in a specially constructed case, and the male on being introduced proceeded as usual, getting more and more excited (even before any visible movement had been made by the female, who was in her retreat). He walked all over the web and into the female's retreat, often spinning threads. The female soon began to move very slowly, following him about wherever he went and showing no signs of hostility to him (though she had driven away a male some days before). He retreated at first whenever he touched her, but after about an hour of this behaviour seemed less afraid of her. He would stand on some of the threads he had made, making his plucking movements, which would become more and more violent and then suddenly cease, only to be renewed again almost at once. The female meanwhile slowly approached him (inverted) waving her fore legs. At first he retreated on contact, but eventually caressed her and made a dab at the *left* of her epigynum with his *left* palp, approaching her from the *side*. (She was inverted in the web, while he was upright.) He retreated at once, and in about half an hour's time (during which neither spider stopped moving) again approached her (as she was approaching him) and again made a dab, this time with his *right* palp on her right and from the *side*. This action at once caused the female to attack him, and he ran away. I left them soon after this, and the female was eating the male the next morning.

The courtship here appears to be analogous to those of Attidæ and Lycosidæ, and by it the male stimulates the female

* They may not be the same males of course, although I have kept males in captivity for two and three months.

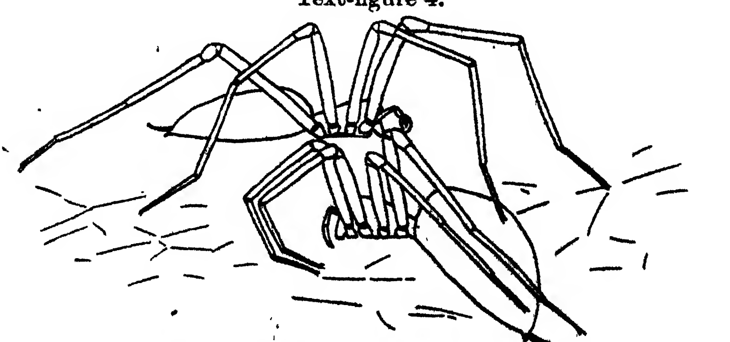
sufficiently to allow him to approach. Also the excitement which the male appears to *induce in himself* seems to suppress his initial fear of the female. The conflict between sex reactions and fear reactions (the latter gradually giving place to the former) is most striking, and the way in which the sexual movements increase in intensity and then suddenly cease probably indicates that the sex emotion has been temporarily dissipated by part of its physical expression. (*Cf.* the habit of many female spiders of eating the males *after* mating.) Such psychological conflict has been observed in higher animals, for instance in the Red-throated Diver by Professor J. S. Huxley (1922). In that case the conflict was between maternal instinct, which stimulated the mother to anger against an intruder, and fear. As soon as anger was dissipated by an attack, fear became dominant and led to rapid flight.

The male of *Amaurobius similis* is stimulated by the female's empty web (even when the female had been absent nearly a month), and goes through all his usual movements, but they are not continued for any length of time unless she is there. Whatever it is that stimulates the male is intimately connected with the *threads* of the female, since several males when put into a box recently occupied by a female, whose spinners had been covered with collodion, showed no sexual reactions, even when the female was put back. The male of *A. ferox* makes similar but more spasmodic movements, and the female I have never found to kill him, though one pair were in the same box for nearly a month.

AGELENA LABYRINTHICA (Clerck).

The mating of this species was observed by Menge (1843) and that of *A. nævia* by Montgomery (1903) and MacCook (1890).

Text-figure 4.



*Agelena labyrinthica.* Showing how ♂ carried ♀.
(Limbs on near side only are drawn.)

In both cases the same thing happens; the male taps the web with his palps as he approaches the female (*cf.* Campbell on

*Tegenaria guyonii* (1882)), who, on being touched on her abdomen, draws her legs up and remains motionless as though "feigning death" (which *A. labyrinthica* does not do normally). She remains like this as long as the male is touching her. With the specimens I watched, the male carried the female about by seizing the femora of her 3rd and 4th legs in his jaws (text-fig. 4). Twice he carried her down the funnel-shaped tube at the corner of the web (observed also by Menge), but mating took place on the sheet. The rigid motionless state of the female is most striking. When they separated she immediately "awoke" and chased the male about the web whenever he approached. She then went through a curious motion that Mr. W. S. Bristowe and I have observed repeatedly amongst Lycosidæ. The legs of each adjacent pair were rubbed violently together in turns. This has not previously been observed in a *female* spider, and its significance is at present obscure. On the day following these observations the female ate the male (also recorded by Montgomery for *A. nævia*).

## General Considerations.

The facts so far discovered about the mating of web-spinners make it clear that, as pointed out by the Peckhams (1889) and MacCook (1890), courtship exists among these spiders and is carried on by vibrations of lines connecting the male and female. In a paper just published, Mr. W. S. Bristowe and I have concluded that among Lycosidæ the function of the male's display is to make himself recognized by the female and to arouse her sexual desires to such a pitch that he may approach her for mating, and that failure to make himself recognized by an adequate display may have fatal consequences for him. Berland observed (1911) that the female of *Dysdera erythrina* becomes less agressive after caressess by the male. Such caresses always precede copulation in spiders, and constitute what we may call a "pre-coition courtship" as distinct from the display-courtship, which comes first (be it a true display or a "tactile display" having the same function).

Mr. W. S. Bristowe (1926) in discussing hearing in web-spinners says:—"Spiders whether they can hear or not can differentiate between the different kinds of vibrations set up in the web. This fact is of considerable importance to the male spider, whose distinctive 'tweaks' and shakings are immediately recognized by the female." He further makes the very interesting suggestion that in males of Theridiidæ possessing a "stridulating organ," vibrations from it pass through their legs and thus along the threads to the female.

In *Amaurobius similis* the display-courtship (which is, of course, tactile) is marked, and there is no doubt whatever that its function is to arouse and keep dominant the female's sexual desires, and probably also to bring her out of her retreat. A

similar sort of courtship is recorded by Berland (1911) for *Filistata insidiatrix*, whose habits and economy are somewhat similar to those of *Amaurobius*.

Turning now to the other cases, one of the most striking facts is the part played by the female. Her obvious state of excitement is shown in *Theridion sisyphium* by her continuous movements, in *Epeira cucurbitina* and *Zilla x-notata* and *Steatoda bipunctata* by her plucking movements and her approaches to the male and by pulsations of the abdomen, and probably by the extension, on the male's approach, of part of the epigynum in *Linyphia leprosa*. Her whole attitude is, in fact, one of complete readiness and eagerness for mating. Consequently the male's tactile display, although necessary (since the male must be *recognized as such*, lest he be attacked), is much diminished, and has only a kind of trigger-action on the female, whose movements now not only guide the male to her, but stimulate him in turn. Males of *Theridion sisyphium*, *Linyphia triangularis*, *Zilla x-notata*, and *Amaurobius similis* (and probably many others) are excited by the empty web of a female; but the excitement soon dies down, the male apparently requiring a further stimulus from the female to proceed with his courtship. In some cases mating has to take place in a peculiar way, *e. g.* on lines constructed previously by the male, as in *Epeira cucurbitina* (*cf.* also *Uloborus plumipes*, studied by Jeanne Berland, (1914)), or the female has to come out from a retreat, as in *Zilla x-notata* (and possibly *Amaurobius similis*); in such cases the tactile display by the male is more marked and may be prolonged, although the female from the start shows no hostility.

Corresponding to the easily-aroused sexual desires of the females of many species, we find that there is no hostility to the male before mating. Many cases are on record of females eating their mates after coition, but authentic cases of their doing so *beforehand* are rare, and are usually found among species where the breeding-season is long (e. g. *Amaurobius*, September to March or longer, and *Tegenaria* (Campbell, 1882), August to October and probably longer *), and where, consequently, a mature female may not be, at any particular moment, in a state to recognize a male. Apparent exceptions are found in some Argiopidæ, such as *Argiope cophinaria* (studied by MacCook (1890)) and notably *Nephila maculata* (Hingston, 1923). The male or males remain on the outskirts of the female's web for some time, and often at first she will not allow them to approach, and may attack them. But after a time her hostility wears off, and then she will only attack males after mating. No marked tactile display appears to take place here, and I think that the female becomes ready for the male at a particular stage in the development of the eggs.

In cases where the mating period is short, females seem to

* I have often found mature males wandering in April.

lose their sexual desires directly after mating and then often attack the male, who, if he escapes, wanders from female to female. Her desires may return, and other males may accomplish mating with her, but for the time being she does not recognize males as such. Here again, it seems, we have a case comparable to that of the Red-throated Diver observed by Huxley and van Oordt (*v.* above under *Amaurobius similis*). Once the sex emotions of the female spider have been dissipated by mating, her normal aggressiveness reasserts itself for the time being, just as when the mother Diver had found expression for her maternal emotions, fear became dominant.

In other cases (e. g. *Agelena*) the female will tolerate a male after mating, sometimes up to the egg-laying and longer, but even so is liable to attack him. We have records of males and females of several other species living together, e. g. *Tegenaria* (Campbell, 1882) from August to October (in which, however, the male "never ceased paying unrequited attentions, except to feed") and *Epeira quadrata*, of which Menge (1866) found 5 nests with the two sexes living together; MacCook (1890) records the same thing of *Epeira insularis* and *E. trifolium*, but regards it as exceptional. Again, Enoch (1885) mentions a pair of *Atypus affinis* which lived together from October to July. Males of *Linyphia triangularis* are found in the female's webs, and they may feed there, and the male of *Steatoda bipunctata* I have never seen attacked at all*. The extreme case is that of *Dictyna*, where the two spiders lead a common life, both taking part in spinning the web and capturing flies; but even here the male probably wanders from female to female, and there is no true family or social life, the young when hatched soon disperse, and are not fed or attended in any way by the parents. If food is plentiful the female will lay several batches of eggs, and may require repeated or prolonged fertilization (though practically nothing is known about this)†. Her predacious reactions will be more ready to give place, under these conditions, to sexual ones, and the male may remain with her in safety for a long time; but, even so, if food is scarce she may attack him. At the best, the relationship between male and female is a loose one, and seems to depend on direct sexual stimuli, which the male almost certainly derives in great part from the female's threads, and I think that she in turn may be stimulated by his. If this is so, it gives us a possible explanation of the apparently aimless way in

* One reason for the immunity from the attacks of females of males which are not courting continually is probably that they "know how to behave" in the female's web. Mr. Bristowe (1926) records an interesting experiment with a specimen of *Amaurobius similis*, which would not attack a wriggling beetle larva until a vibrating tuning-fork was placed in the web beside it. Spiders always attack a buzzing insect more readily than one just wriggling, and a male's movements, apart from those involved in his courtship, are not likely to excite the female very much, particularly as he often remains motionless for long periods.

† Subsequent work has shown that once the female has been impregnated all her eggs hatch, so that further mating seems unnecessary.

which many males spin threads in the webs of the females they are courting (e.g. *Steatoda bipunctata*, *Amaurobius similis*, *A. ferox*, and *Linyphia clathrata*). But, further, if the stimulus from threads is sufficient (particularly in a case like *Dictyna*, where the male spins a great deal of the web but shows no very marked tactile display), it may serve to keep male and female together and be the basis of their common life. Such a state of affairs is comparable to Wheeler's "trophallaxis" among social wasps and ants, and Professor J. S. Huxley has proposed the term "erotallaxis" for it. Its function is, however, limited to mating, since the parents do not co-operate in any way in tending the young.

There is one other point that arises, and that is the condition of the female spiders during the actual act of mating. Without exception they are (in web-spinners) in a state of complete immobility at these times, which, is, of course, essential to the proper completion to the act.

We must distinguish between the extreme cases of *Epeira cucurbitina* and *Agelena labyrinthica*, where the female is in a contracted immobile state before copulation begins, and those of *Theridion sisyphium*, *T. denticulatum*, *Zilla x-notata*, etc., where rigidity is only produced when the male's palp is actually applied; and finally there are other cases where there is no rigidity but nevertheless immobility (e.g. *Linyphia triangularis*, *L. clathrata*, *L. leprosa*, *Dictyna*, *Theridion lineatum*, and *Steatoda bipunctata*).

This curious cataleptic condition of the female is probably induced by the pre-coition caresses of the male or by the application of his palp. A very similar, if not identical, condition is that of spiders when "feigning death" (an unfortunate term, since the attitudes assumed are rarely those of the dead animals). The Peckhams, who conducted experiments (1887) on "feigning death" with several spiders (especially *Epeira bombycinaria*, *E. infumata*, and *E. insularis*), were of the opinion that it was produced by natural selection, since it was of use to the spiders in which it occurs (Epeiridæ, Theridiidæ, Linyphiidæ, and many other sedentary spiders) for escaping from enemies; whereas in the species that run about (Attidæ and Lycosidæ) it does not occur. This explanation may be true, but it is curious to note that the females of *Agelena labyrinthica* and *A. nævia*, which do not "feign death" when frightened or touched, assume a cataleptic condition while mating.

In all these cases the motionless condition of the female has a useful function, for it enables the male to keep his style fixed in the female's epigynum, which he could not do if she were still making her excited movements. In *Tarentula barbipes* the female remains still during copulation (which is short) and then usually struggles free: in *Lycosa*, copulation lasts a long while, and the female carries the male about; so here again he has no difficulty. In all web-spinners I have watched there is no close embrace, but the difficulty is overcome by the female's immobility or rigidity.

In this connection it is extremely interesting to note the habit of the Solpuga, *Galeodes caspius turkestanus*, observed by Heymons (1901). The male seizes the female sharply in the dorsal part of the abdomen, whereupon she remains motionless during the mating and until he runs away. It is possible to induce the condition artificially, *but only in females ready for fertilization*. (I have not seen the original paper where these observations are recorded, but they are quoted in "Hypnose und Katalepsie bei Tieren," by Ernst Mangold (Fischer: Jena, 1914).)

## Summary.

(1) A tactile display may occur in web-spinners analogous to the visual display of the Attidæ and Lycosidæ and having the same function (e. g. *Amaurobius similis*).

(2) The female may be ready for the male on his approach and show him no hostility (usually the case with species with a short mating period); the tactile display is now reduced and has a kind of trigger-action. If, in these cases, a female must be induced to come out of a retreat or onto special threads, the tactile display is more marked.

(3) Females usually attack males *after* mating, but in some species tolerate them, when, if food is plentiful, a common life may occur.

(4) In some species, males react to threads left by the female and even to those of another male. Possibly threads of males (often spun in female's webs) stimulate females, which would be a factor in the common life of species such as *Dictyna*, and may be a part of the courtship in other cases.

(5) All females remain motionless during copulation and some assume a rigid cataleptic condition, induced probably by the male's pre-coition caresses or by the introduction of his style into the epigynum.

In conclusion, I wish to express my thanks to Professor J. S. Huxley for much valuable advice and encouragement with regard to this paper, to Mr. W. S. Bristowe for allowing me to add his notes to my own and for many helpful criticisms, and to Dr. A. R. Jackson, who has very kindly classified many of my specimens from time to time.

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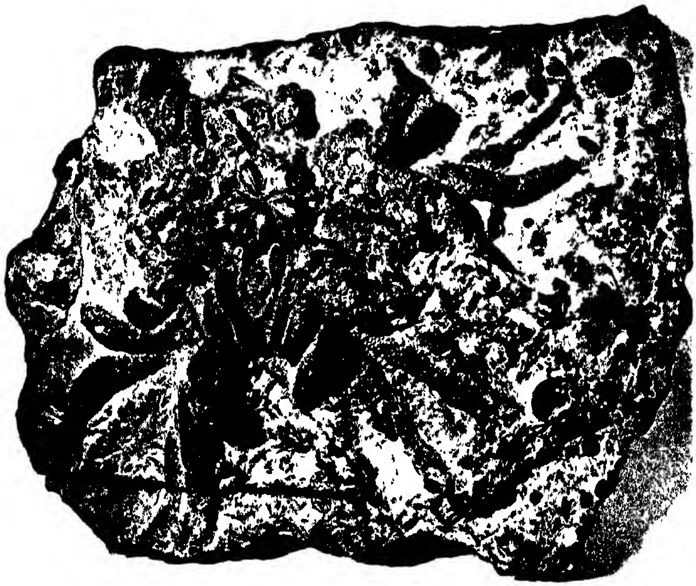

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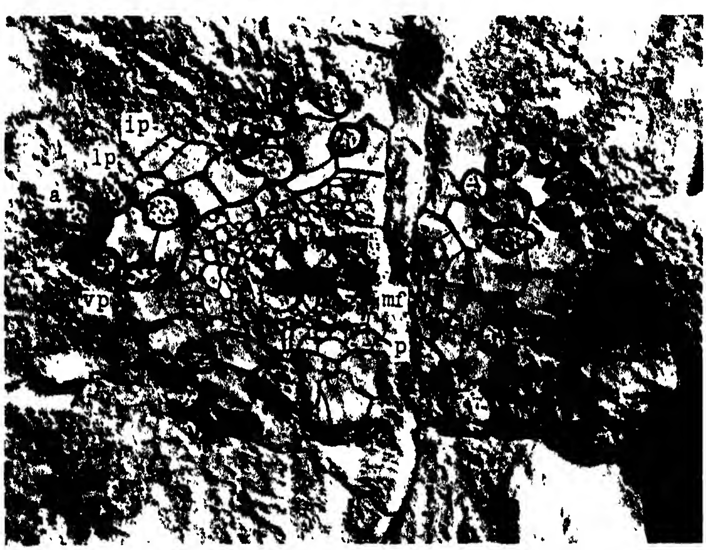


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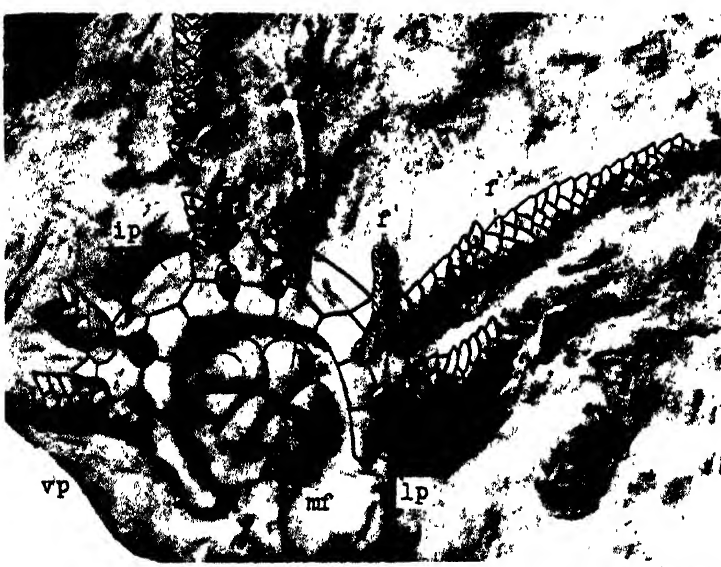
2.

I. EUCLADIA JOHNSONI. 2 SOLLASINA WOODWARDI.

1.

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1. SOLLASINA WOODWARDI. 2. EUTHEMON IGERNA.

# 59. The Plan of Structure and Systematic Status of the *Ophiocistia* (Echinoderma). By Prof. D. M. Fedotov, Zoological Laboratory, Academy of Sciences, Leningrad *.

[Received May 20, 1926: Read October 19, 1926.]

(Plates I., II.; Text-figures 1, 2.)

## *Introduction.*

This paper discusses the morphology of the group Ophiocistia of Sollas and its place in the system of Echinoderma. The views on this group expressed in my paper on the morphology of the Euryalæ (Fedotov, 1926) were based on a misinterpretation of the data of Prof. Sollas, and are therefore changed. It is not necessary to give a full review of the literature, since the main difficulty lies in the correct interpretation of the appendages.

According to Woodward (1869) and Gregory (1896) *Eucladia johnsoni* had bifurcated or branched arms, while Gregory described also the vertebral ossicles with streptospondyline articulation, but Sollas (1899) proved these data to be incorrect. Dr. Bather (1907, p. 70, 1910, p. 880, also in Sedgwick, 1909, p. 206) made the correct suggestion that the appendages of these forms correspond to the podia or tube-feet and that the plates of the body of Ophiocistia correspond to the arm-plates of Ophiuroidea. Unfortunately Bather's opinion, though fully expressed for the past twenty-five years in the printed labels of the British Museum, has been overlooked by later authors. The true nature of the appendages being thus ignored, the systematic position of these forms remained obscure. Since Woodward's paper (1869) *Eucladia* was referred to Palæ-Euryalæ (Stürtz, 1893). Gregory established a new family Eucladidæ, which he included in the order Streptophiuræ. Sollas (1899), who described two more new forms, erected for all of them the order Ophiocistia of the same value as Euryalæ, but later (1912) he regarded it as a distinct class of Echinoderma, possibly allied to the Ophiuroidea. Schuchert (1915) on the whole agreed with Sollas. In my former paper (1926) I doubted if *Euthemon igerna* were a brittle-star and regarded the restoration of *Eucladia woodwardi* by Sollas as improbable. I left the order Ophiocistia only for *Eucladia johnsoni*, while admitting that *Eucladia? beecheri* (Schuchert, 1915, pp. 278–279, pl. 38, fig. 1) might be a member of group Euryalæ. Those views were based on the insufficient illustrations and contradictory descriptions of the authors, which made it almost impossible

* Communicated by Dr. F. A. Bather, F.R.S., F.Z.S.

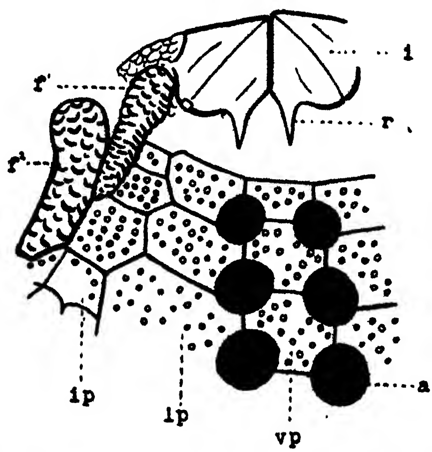
to understand correctly the highly peculiar structure of these forms. Only after a personal study of the original material, which is in the British Museum (Nat. Hist.), and in the Oxford University Museum, am I able to give what I consider to be the true interpretation of the structure of Ophiocistia. To make my views clear, I will give redescriptions or point out some features of the original material, illustrating them by drawings and photographs.

*Full description of* Eucladia johnsoni *H. Woodward.*
(Plate I. fig. 1; text-figs. 1, 2.)

Unique holotype in the British Museum (Nat. Hist.), E 1444; Middle Silurian, Lower Ludlow Shales, Sedgley, near Dudley.

Body discoidal, oval, slightly quinque-lobate, comparatively thick (at least 1·3 mm.) (Pl. I. fig. 1); its largest diameter,

Text-figure 1.



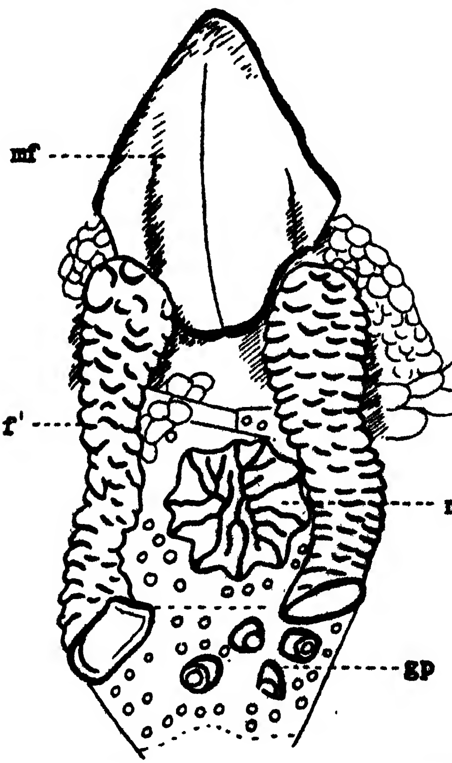

*Eucladia johnsoni.* Diagram of one ray in the oral part of the disc (NE region of Pl. I. fig. 1): *a*, apertures of podia ($f^1, f^2$); *ip, lp, vp*, interradial, adradial, and perradial plates; *i*, interradial, and *r*, radial, elements of the mouth-frames. × 2.

about 5 cm., the shortest one, 4 cm. No arms; in each radius on the oral surface seven pairs of the appendages. Oral surface covered with numerous polygonal large plates with granulæ (text-fig. 1). The plates are somewhat like the plates of the test of Echinoidea. Dorsal surface unknown, but it is probable that the whole body was covered by a test. In the centre of the oral surface (Pl. I. fig. 1) there is a pentagonal rosette of five strong pieces (plates) interradial in position. In each of the

pieces (text-fig. 2, *mf*) one can distinguish two interradial parts (text-fig. 1, *i*) and two radial parts (*r*) (projecting portions of the latter were called by Woodward "styliform processes," 1869, p. 242). They may be regarded as the mouth-frames (*mf*). Judging by the deep hollows between the mouth-frames and the body and by presence of skin of the peristome around the mouth-frames, it may be assumed that the mouth-frames were retractile. It is very difficult to make an exact and exhaustive description of the plates of the disc because it is partly hidden by the appendages and partly badly preserved, especially near the buccal armature. Besides, some of the plates are displaced. The radial areas are wide, the interradial narrow. Beginning with the second pair of appendages or podia (text-fig. 1, $f^2$), there are in each radial area one column of median or perradial plates (*vp*), and two columns of lateral or adradial plates (*lp*). These three columns together represent the radial area of the test and they surround circular apertures or pores (*a*) for the podia as in Ophiuroidea, but each pore is bounded by two perradial and two adradial plates. The plates are firmly united, the sutures of the perradial plates being hardly perceptible. The rows of perradial plates are narrow and the plates (*vp*) are strongly cut into by apertures. The adradial plates (*lp*) are polygonal, strongly expanded transversely, and meet the plates (*ip*) of the interradius. The interradial plates (text-fig. 1, *ip*) are placed in a single column of four plates, beyond which there is apparently a pair of plates. The adoral (first) plate of the column is smallest. On the second plate in one of the interradii lies a large madreporite (text-fig. 2, *m*), its surface covered by irregularly dichotomously branched furrows as in the recent starfishes (e.g. *Asterias rubens*), though the furrows in *Eucladia johnsoni* are not so numerous as in *Asterias*. On the next plate there are four prominent papillæ, as they were called by Woodward, but they probably represent the genital pores (text-fig. 2, *gp*) because they have a cavity filled with matrix; if so, it may be assumed that *E. johnsoni* had an unpaired gonad. The boundaries of the plates with the madreporite and genital pores are indistinct. The appendages of the first pair (Pl. I. fig. 1) are much smaller than the others (about 9 mm. in length and 2 mm. in breadth). They lie somewhat apart from the others in the angle between the radial and interradial parts of the mouth-frames in the region of the disc covered by skin. They correspond to the oral feet of starfishes and brittle-stars. The appendages of the first pair are opposite, the others are slightly alternating as the tube-feet in the Asteroidea. The following six pairs of the appendages are close to each other. The appendages increase in size from the centre of the disc to its periphery. The length of the largest is about 40 mm., its breadth about 5 mm. It is quite clear from the position of the appendages that they are homologous with the podia or ambulacral feet. The

appendages as pointed out by Sollas (1899) were hollow and their cavities are filled with matrix. They were apparently flexible, and their surface is covered by spiny scales which give them a scabrous appearance, as described by Woodward. The first pair of appendages is preserved best, some of them

Text-figure 2.




*Eucladia johnsoni*. Diagram of the adoral part of the interradius next the observer in Pl. I. fig. 1, with madreporite (*m*) and genital pores (*gp*); *f*, oral feet; *mf*, mouth-frames. × 4.

being quite complete with a sucker or flattened expansion on the end. By analogy with the first pair, we may assume that all the appendages had such soles, and they may be regarded as true ambulacral feet or podia, but enormously developed. Thus Bather's interpretation of the appendages is quite correct. Very probably the appendages were used as walking feet.

### *Morphological Interpretation of some Features of the other Species.*

I will not give full descriptions of *Eucladia woodwardi* Sollas and *Euthemon igerna* Sollas, because I found the description by Prof. Sollas correct, but will point out only some features of their structure. It is necessary to illustrate my interpretation by photographs and drawings because Sollas has given only restorations. I will not consider the structure and systematic position of *Eucladia? beecheri* Schuchert (1915, pp. 278–279, pl. 38. fig. 1) because too little is known about this form and I have not studied it personally.

It is easy to see, that the five plates (*mf*), paired in origin, interradial in position, in the centre of the oral surface of the disc of *Eucladia woodwardi* (Pl. I. fig. 2) and *Euthemon igerna* (Pl. II. fig. 2) represent the mouth-frames. Each of them apparently consists of two interradial and two radial elements (*E. igerna*, Pl. II. fig. 2, *mf*). The peristome in *E. woodwardi* (Pl. I. fig. 2, *p*) is very well developed. Since the mouth-frames in *E. igerna* (Pl. II. fig. 2, *mf*) are sunk into the test and the margin of the test around the mouth-frames is regular, it follows that there also was peristome, as suggested by Sollas. It is clear that the mouth-frames of both forms were retractile.

A column of median or perradial plates (Pl. I. fig. 2, Pl. II. fig. 2. *vp*) and two columns of lateral or adradial plates (Pl. I. fig. 2, Pl. II. fig. 2, *lp*) in each radial area correspond to the plates of the radial areas of *Eucladia johnsoni* and to the ventral and lateral plates of the recent Ophiuroidea. Perradial and adradial plates limit the apertures or pores for the appendages in each radial area, similarly to the arrangement in Ophiuroidea, but each pore (*a*) is bounded by two perradial and two adradial plates The appendages (Pl. II. figs. 1, 2, $f^1, f^2$) are superficially similar in their shape, in the shape and arrangement of the plates (dorsal, ventral, and two lateral rows) to the arms of recent Ophiuroidea. But from the relation of the appendages to the disc and its skeleton and from the absence (very probably) of the vertebral ossicles, it is evident that the appendages are homologous not with arms but with podia. It is probable that the appendages of these forms had wriggling movements like the arms of Ophiuroidea. Perhaps they were used also as the cirri of Crinoidea. The small appendages of the first pair in *Euthemon igerna* (Pl. II. fig. 2, $f^1$) may have been an organ of sense. The dorsal surface of the body of *Eucladia woodwardi* (Pl. II. fig. 1) with its numerous imbricated irregularly polygonal plates corresponds to the dorsal surface of the disc of Ophiuroidea, but the skeleton is different.

The differences between *Eucladia johnsoni* and *Eucladia woodwardi* are too great to consider the two species congeneric. I will point out only the more important features of *Eucladia woodwardi* which are at least of generic value. The shape

of the body, the external skeleton of the oral surface of a small number of plates, well-developed peristome, structure and arrangement of the appendages, absence of madreporite and genital pores in one of the interradii, quite different principle of progression, probably by wriggling movement of the appendages, are characters amply sufficient for the establishment of a new genus to include this form. I propose to call it SOLLASINA in honour of Professor Sollas. Moreover, it is obvious that *Sollasina woodwardi* and *Euthemon igerna* are nearer to each other than to *Eucladia johnsoni*, and cannot be retained in the same family of the latter (fam. Eucladidæ). Thus it is necessary to establish a new family Sollasinidæ with two genera, *Sollasina* and *Euthemon*.

*Discussion.*

The discoidal central body without arms is the most important feature of these forms. Its skeleton, as suggested by Dr. Bather, may be compared with the skeleton of the disc of Ophiuroidea. The single column of median or perradial plates and two columns of lateral or adradial plates are homologous with the ventral and lateral plates of Ophiuroidea. The plates along the median line of the interradial area of Ophiocistia correspond to the skeleton of the interbrachial area of Ophiuroidea. The difference in the structure of the oral surface of the disc of Ophiocistia and of Ophiuroidea is as follows:—The interradial area of Ophiocistia is narrow, its greater part formed by lateral or adradial plates of radii, while in Ophiuroidea the lateral plates are narrow, small, the radial parts of the disc are narrow, and the interbrachial (interradial) parts are wide. There is a certain analogy between the Ophiocistia and *Astrophiura* as Prof. Sollas already pointed out (1899, p. 699,—*Astrophiura permira* Sladen, 1879), but a still more complete analogy exists between Ophiocistia and *Astrophiura kawamuri* Matsumoto, in which the lateral plates of the basal segments of the arms also cover the greater part of the interbrachial area (Matsumoto, 1917, p. 271, fig. 68 *b*). The plates of the dorsal surface of Ophiocistia are known only in *Sollasina woodwardi*, and they differ from those in Ophiuroidea by absence of primary plates and by their irregular arrangement. There is no analogy between the dorsal surface of the disc of Ophiocistia and *Astrophiura*, because the large pentagonal body of *Astrophiura* consists of the disc proper and of dorsal and very strongly expanded lateral plates of arms (Sladen, 1879, pl. xx. figs. 3, 7; Koehler, 1915, p. 3, fig. 1; Matsumoto, 1917, p. 241, fig. 68 *a*), so that a large size of the body is a secondary feature. In Ophiocistia only the disc is present but no arms, and the large size of the disc is a primary feature. It can be accepted that the radial parts of the oral surface of the disc of Ophiocistia are homologous with the basal segments of radii of recent Ophiuroidea; their

paired appendages protruding through the pores between the lateral and ventral plates are homologous, as suggested by Bather, with podia. There is, however, a great difference between the various Ophiocistia. *Eucladia johnsoni* has very large podia with curious scales, with suckers or soles; they resemble the tube-feet of Asteroidea in the general principle of the structure, arrangement (slightly alternating) and in function. The podia of the other Ophiocistia are also very large, with a regular external skeleton strongly similar to that of the arms of recent Ophiuroidea. It is interesting that the majority of Palæozoic Ophiuroidea (Matsumoto, 1917, p. 5, pp. 367-368; Spencer, 1925, p. 258) had no ventral or dorsal arm-plates, but many of them had the ambulacral feet large though typical in structure. The Silurian Ophiocistia had no arms, but their enormous podia had the plates such as can only be seen on arms of the modern Ophiuroidea.

It is very difficult to make a detailed comparison between the mouth apparatus of the Ophiocistia and of Ophiuroidea. The five pieces or plates of the rosette of Ophiocistia may be regarded as mouth frames. It is very probable that each consists of two interradial and two radial elements. But the mouth-frames of Ophiocistia had some peculiar features. They were more compact than those of Ophiuroidea and Asteroidea. The whole mouth apparatus was more independent of the skeleton of the body. Probably it had a masticating function. The presence of a peristomial membrane indicates that the mouth-frames were retractile. Thus the mouth apparatus of Ophiocistia reminds one somewhat of that of Echinoidea.

The presence of a large madreporite in *Eucladia johnsoni* and its absence from *Sollasina woodwardi* and *Euthemon igerna* probably are in connection with a walking function and wriggling movements of their respective appendages.

It is very interesting that on the whole Ophiocistia had a general resemblance to the very young of Ophiuroidea, Asteroidea, and Echinoidea. The latter has a discoidal body consisting of oral and apical parts, no arms, but with a few pairs of very large tube-feet (Ludwig, 1882, Lovén, 1892, Bury, 1895, McBride, 1907). Later on the starfishes develop the arms, the body acquires the star-like shape. In Echinoidea the oral part of the disc develops very strongly so that the apical part becomes a small apical field of the test. In Ophiuroidea the central disc acquires long slender arms. A strong development of the interbrachial area leads to a change of the primary structure of the oral surface of the disc. Ophiocistia seem to stop at the stage when the disc consists of equal oral and apical parts, without arms, but with few basal segments of radii, which represent elements of the oral surface of the disc. The unpaired gonad of *Eucladia johnsoni* corresponds to the primary gonad during development of Ophiuroidea,

Asteroidea, and Echinoidea, which later develops into the five pairs of the definitive genital organs.

Thus Ophiocistia differ in the plan of their structure from other classes and may be regarded as a class of Eleutherozoa of the same taxonomic value as Asteroidea and Ophiuroidea, but nearest to the latter as already suggested by Sollas (1912). Ophiocistia are characterised by certain primitive features such as the large disc and the absence of arms, while on the other hand the skeleton of the body, the mouth apparatus, and the appendages are very peculiar and highly developed.

The structure of Ophiocistia tends to confirm Jaekel's opinion (1923, pp. 347–348) that the arms of Ophiuroidea are not radial projections of the disc like the arms of Asteroidea. At the same time it supports the theory of the origin of Eleutherozoa from Pelmatozoa, contrary to the opinion of Barrois, who thought these two types quite independent (Barrois, 1924, p. 400). In fact *Eucladia johnsoni* in the form of the external skeleton, with madreporite and genital pores near the mouth, has general resemblance to the Cystidea.

## Class **Ophiocistia** Sollas, 1899, 1912.

*Diagnosis.* Palæozoic Eleutherozoa in their structure nearest to Ophiuroidea, with discoidal body covered with a test of polygonal plates, without arms. Radial areas of the oral surface wide, and each consisting of one column of perradial plates (=ventral plates of Ophiuroidea) and two columns of adradial plates (=lateral plates of Ophiuroidea); interradial areas narrow and each with one column of interradial plates. Pentagonal rosette of five mouth-frames lies in peristome; mouth-frames strong, compact, retractile, interradial in position. Several pairs of huge podia, probably with either walking or wriggling movement, on oral surface of each radial area. Each podial pore limited by two perradial and two adradial plates. Anus apparently absent.

### 1. Family Eucladidæ Gregory, 1896.

*Diagnosis.* Discoidal body slightly quinque-lobate, covered with a test of numerous plates. Peristome not very well developed, about 2/5 of diameter. Margin of the test around the mouth-frames consists of twenty plates; five perradial, ten adradial, and five interradial. Podia (probably all) with suckers, slightly alternating and used for walking as in Asteroidea, covered with spiny scales. One of the interradii on oral surface bears a large separate madreporite and several genital pores.

### Genus Eucladia Woodward, 1869.

*Diagnosis.* The plates of the test with large granules. At least seven plates in each column of the radial areas and

five or six plates in each interradial area. Mouth-frames strong, large, occupying almost the whole peristome. Seven pairs of podia in each radius; the first pair are small oral feet, the other six pair huge, increasing in size from the centre of the disc to its periphery. Genital pores four, surface of madreporite with dichotomously branching furrows.

Genotype: *E. johnsoni* Woodward. (Pl. I. fig. 1; text-figs. 1, 2.) Woodward, H., 1869, Geol. Mag., dec. i. vol. vi. pp. 241–243, pl. viii.; Gregory, 1896, Proc. Zool. Soc. pp. 1040–1042; Sollas, W. J., 1899, Quart. Journ. Geol. Soc. vol. lv. pp. 692–693.

*Material.* Unique holotype in the British Museum (Nat. Hist.), E. 1444; Middle Silurian, Lower Ludlow Shales, Sedgley, near Dudley.

This is the only known species.

## 2. Family SOLLASINIDÆ, nov.

*Diagnosis.* Discoidal body non-lobate, covered with a test of small number of plates. Peristome well developed, at least 1/2 of diameter. Margin of the test around the mouth-frames consists of fifteen plates: five perradial and ten adradial. Podia tapering to the ends, opposite, covered with regular skeleton of dorsal, ventral, and two lateral rows of plates, superficially like the arm-plates of Ophiuroidea; movement probably wriggling. In oral surface of the disc neither separate madreporite nor genital pores.

### 1. Genus SOLLASINA, nov.

*Diagnosis.* Body-outline oval; test flexible, of imbricated plates with minute granules. In each radial area one column of three perradial plates and two columns of probably three adradial plates; two plates in each interradial area. Peristome large, oval; peristomial membrane with small, irregular plates. Mouth-frames comparatively small. Three pairs of huge podia in each radius, nearly equal in size, like arms of Ophiuroidea. Dorsal surface of the disc covered with numerous, imbricated, irregularly polygonal plates.

Genotype: *S. woodwardi* (Sollas). (Pl. I. fig. 2, Pl. II. fig. 1.) *Eucladia woodwardi*, Sollas, W. J., 1899, Quart. Journ. Geol. Soc. vol. lv. pp. 695–696, figs. 1, 2.

*Material.* Lectoholotype (Pl. I. fig. 2), Oxford University Museum; paratypes: eight specimens in the Oxford University Museum, one specimen in the British Museum (Nat. Hist.), 57780, from Middle Silurian, Lower Ludlow, Church Hill, Leintwardine.

### 2. Genus EUTHEMON Sollas, 1899.

*Diagnosis.* Body depressed sphæroidal, subpentagonal, with a firm test of strong, smooth plates. In each radial area one

column of three perradial and two columns of probably three adradial plates. One plate in the interradial area. Peristome large, round; mouth-frames large, strong. Two pairs of podia in each radius, the first small, the second very large; they are superficially like arms of Ophiuroidea.

Genotype: *E. igerna* Sollas. (Pl. II. fig. 2.) Sollas, W. J., 1899, Quart. Journ. Geol. Soc. vol. lv. pp. 696–699, figs. 3, 4.

*Material.* Unique holotype in the Oxford University Museum; Wenlock Limestone, Croft Farm, Malvern.

I would like to express my sincere thanks to Prof. Sollas, Dr. F. A. Bather, and Mr. T. H. Withers for their kind assistance during my work in the respective Museums. To Dr. F. A. Bather I am much obliged also for his most helpful criticism of my manuscript.

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## EXPLANATION OF THE PLATES.

### Plate I.

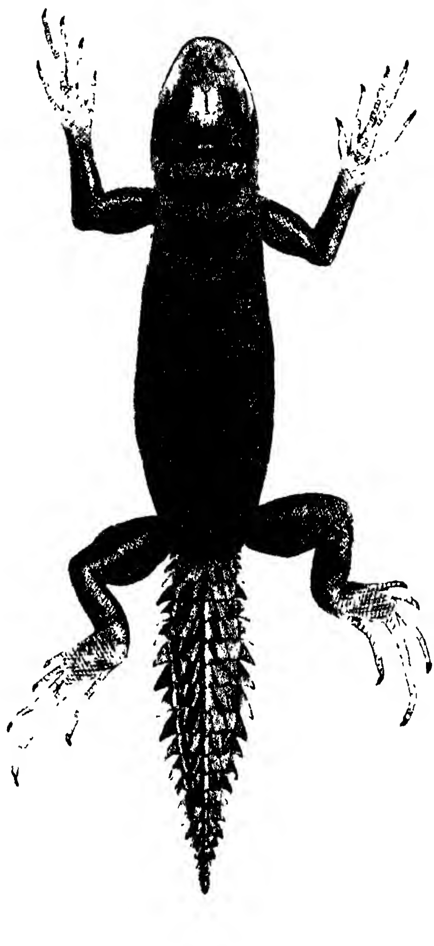
Fig. 1. *Eucladia johnsoni*. Oral surface. (Photograph by Mr. H. G. Herring, supplied by the permission of the Trustees of the British Museum.) $\frac{3}{4}$ nat. size.

Fig. 2. *Sollasina woodwardi*. Oral surface. Diagram based on photograph: *a*, apertures of podia; *ip*, *lp*, *vp*, interradial, adradial, and perradial plates; *mf*, mouth-frames; *p*, peristome. (Photograph by Mr. H. T. Hambridge, supplied by permission of Prof. Sollas). × 3.

### Plate II.

Fig. 1. *Sollasina woodwardi*. Dorsal surface. (Photograph by Mr. Hambridge.) × 2.

Fig. 2. *Euthemon igerna*. Oral surface. Diagram based on photograph. $f^1, f^2$, podia; *ip*, *lp*, *vp*, interradial, adradial, and perradial plates; *mf*, mouth-frames. (Photograph by Mr. Hambridge.) × 6.



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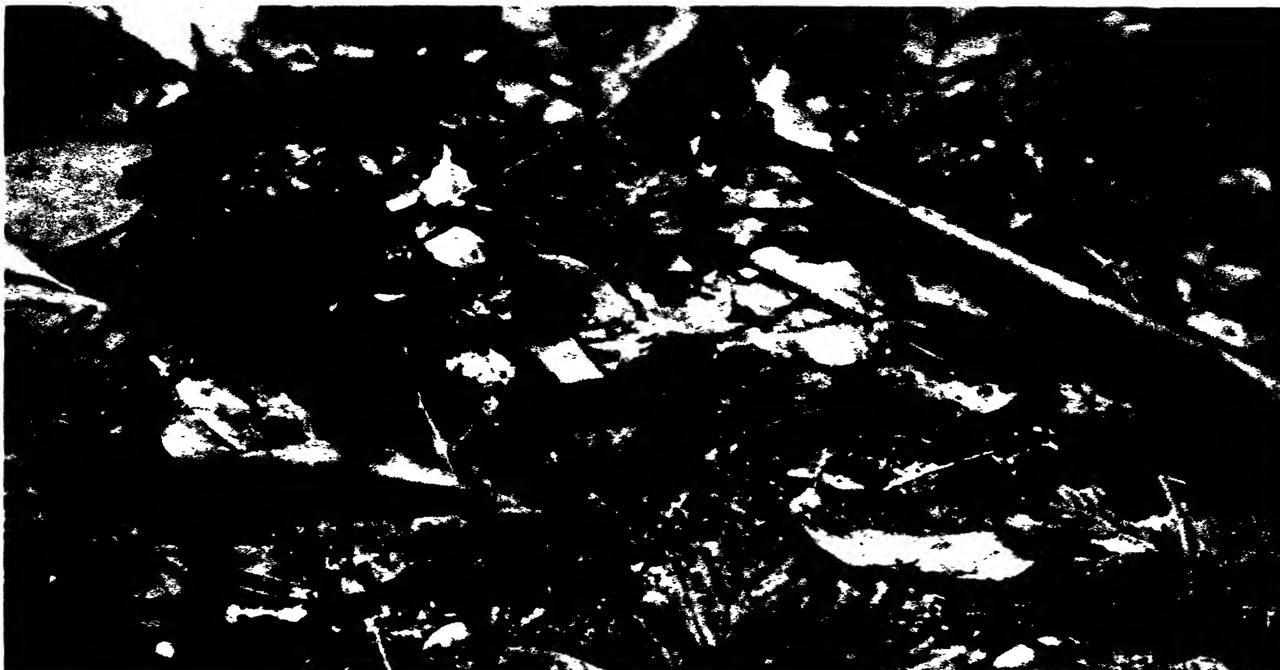
UROCENTRON AZUREUM. ♂ from Marajo Island (Nat size)

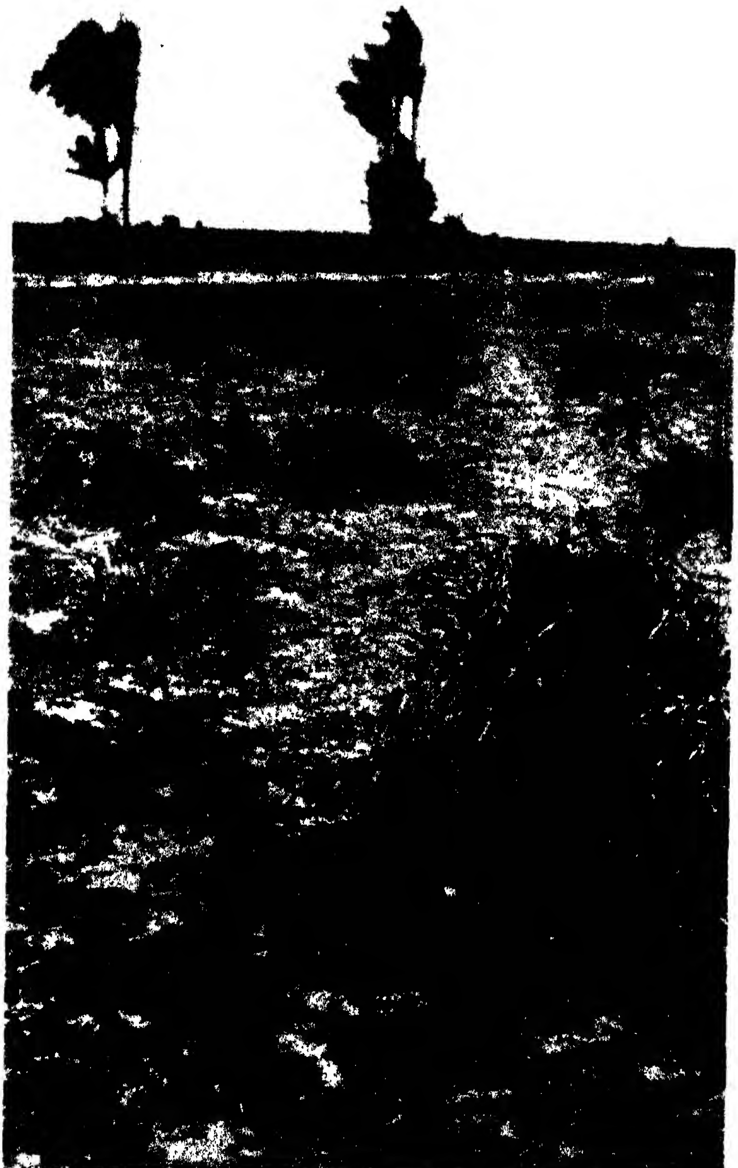


1

1. *Bufo typhonius.*
2. *Polychrus marmoratus.* From a living specimen

*HYLA VENULOSA.* Natural size.
Taken from a living specimen.

Young specimen of *Iguana tuberculata*, from life.



*Cyclagras gigas.*

# 60. Observations on the Life-Habits of some Batrachians and Reptiles from the Lower Amazon: and a Note on some Mammals from Marajó Island. By Hugh B. Cott, B.A., F.Z.S.

(From the University Zoological Laboratory, Cambridge.)

[Received September 6, 1926: Read November 2, 1926.]

(Plates I.–VI.*; Text-figure 1, and Map.)

Contents.



## I. Introductory Note.

These scanty notes are the result of a short trip to the Amazon during the months October 1925 to January 1926. My objects in making the expedition were to obtain a series of photographs of some of the animals inhabiting this wonderful region, to study their life-habits, and to collect zoological specimens for the British Museum (Natural History): it was also hoped to be able to bring home a number of living specimens for the Zoological Gardens.

The following list is a summary of the Batrachia and Reptilia collected:—

## BATRACHIA.

### ANURA.

#### Aglossa.

1. *Pipa pipa* L. — Pará.

#### Bufonidæ.

2. *Bufo marinus* L. — Pará, Marajó Is.
3. *Bufo granulosus* Spix. — Marajó Is.
4. *Bufo typhonius* L. — Pará.

* For explanation of the Plates see p. 1178.

### HYLIDÆ.

| | |
|---|---|
| 5. *Hyla venulosa* Laur. | Pará. |
| 6. *Hyla nasica* Cope. | Pará. |
| 7. *Hyla aurantiaca* Daud. | Itacoatiara. |
| 8. *Hyla rubra* Daud. | Pará, Antonio Lemos, Marajó Is. |
| 9. **Hyla leucophyllata* Beiris. | Pará. |
| 10. *Phyllomedusa burmeisteri* Blgr. | Pará. |

### CYSTIGNATHIDÆ.

| | |
|---|---|
| 11. *Leptodactylus caliginosus* Gir. | Marajó Is. |

## REPTILIA.

### LACERTILIA.

### GECKONIDÆ.

| | |
|---|---|
| 12. †*Thecadactylus rapicaudus* Houtt. | Pará. |
| 13. *Hemidactylus mabouia* Mor. | Marajó Is., Pará. |

### IGUANIDÆ.

| | |
|---|---|
| 14. *Anolis ortonii* Cope. | Itacoatiara. |
| 15. *Anolis fusco-auratus* D'Orb. | Antonio Lemos. |
| 16. *Polychrus marmoratus* L. | Pará. |
| 17. *Tropidurus hispidus* Spix. | Pará. |
| 18. *Uraniscodon umbra* L. | Pará. |
| 19. *Urocentron azureum* L. | Marajó Is. |
| 20. *Iguana tuberculata* Laur. | Marajó Is. |

### TEIIDÆ.

| | |
|---|---|
| 21. *Tupinambis nigropunctatus* Spix. | Marajó Is. |
| 22. *Centropyx calcaratus* Spix. | Antonio Lemos, Pará. |
| 23. *Ameiva ameiva* L. | Itacoatiara, Pará. |

### SCINCIDÆ.

| | |
|---|---|
| 24. *Mabuia aurata* Schn. | Antonio Lemos. |

### OPHIDIA.

### COLUBRIDÆ.

| | |
|---|---|
| 25. *Herpetodryas fuscus fuscus* L. | Pará. |
| 26. *Liophis almadensis* Wagl. | Marajó Is. |
| 27. *Cyclagras gigas* D. & B. | Marajó Is. |
| 28. *Xenodon severus* L. | Pará. |
| 29. *Aporophis lineatus* L. | Marajó Is. |
| 30. *Rhadinæa genimaculata* Bttgr. | Marajó Is. |
| 31. *Oxybelis acuminatus* Wied. | Pará. |

Part of the above material was obtained at stopping places during a river-trip to Manãos, *e. g.*, at Itacoatiara and Antonio Lemos (near Brèves); but the present paper is based entirely on observations made in the following localities:—

(i.) The forest region in the immediate neighbourhood of the Belem (Pará).

(ii.) The campos in the North-East interior of Marajó Island.

* I am indebted to the Rev. A. Miles Moss for a specimen of this handsome little frog, which was taken by him recently in the Bosque, Pará.

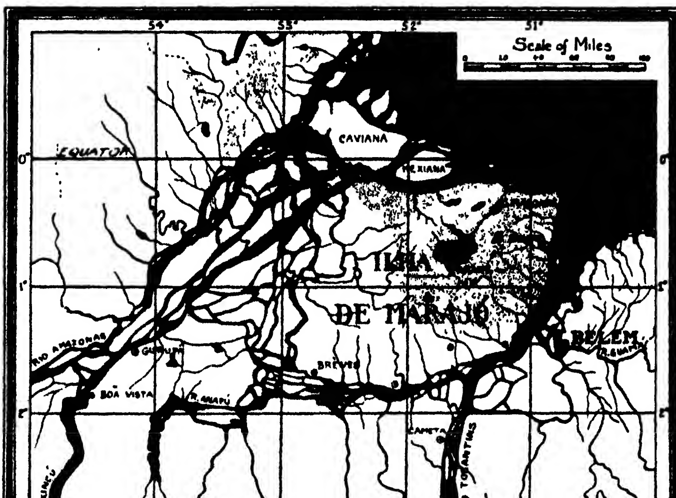
† A specimen of this lizard was taken recently in Pará and kindly sent to me by the Rev. A. Miles Moss.

Marajó Island has received little attention from naturalists in the past.

Situated in the mouth of the Amazon river, it is larger in surface area than Wales; it is approximately equally divided into two œcological districts—that in the south-west consisting of virgin forest, while the north-eastern part (dotted area, *vide* Map) is open "campo," where numerous herds of cattle are reared.

It is not intended to give here a general account of the fauna of the island, but it is worth while to point out briefly, in passing, various respects in which Marajó is remarkable.

The most striking feature about the fauna of the island is the extraordinary abundance of various kinds of animal life. I refer not so much to the number of species as to the great number of




individuals, and it is only the most prominent forms that will be mentioned here.

As regards Reptiles, Marajó Island is noteworthy as being the headquarters and breeding-ground of two species of "Jacarés," *Caiman niger* and *C. sclerops*, both of which occur in incredible numbers. Iguanas (*Iguana tuberculata*) and the so-called "Jacruarú" (*Tupinambis nigropunctatus*) (which is hunted with dogs by the natives) are both very common.

Passing on to the Birds, this is the home of vast numbers of Egrets (*Ardea egretta*), Roseate Spoonbills (*Platalea ajaja*), Scarlet Ibises (*Eudocimus ruber*), and various species of Wild Duck; while the Maguari Stork (*Euxenura maguari*), Jacana (*Parra

*jacana*), the "Teú-teú" (*Vanellus cayennensis*), Turkey-Vulture (*Cathartistes urubu*), Guira Cuckoo (*Guira guira*), American Diver (*Plotus anhinga*), Toucans, Parrots, and Parroquets (especially *Conurus aureus*) are all conspicuously abundant.

The Mammalian Fauna is also interesting, the following species all being tolerably common :—the Jaguar (*Felis onça*), especially in the north and north-east, Kinkajou (*Cercoleptes caudivolvulus*), Coati (*Nasua*), Tamandua (*Tamandua tetradactyla*), Three-toed Sloth (*Bradypus tridactylus*), Peba Armadillo (*Tatusia septemcincta*), and several species of Monkeys, while the "Mucúra" (*Didelphys marsupialis*) is very plentiful. Finally, large herds of Capybaras (*Hydrochœrus capybara*) live by the lakes on the campo, which is also inhabited by vast numbers of Bats (notab y *Noctilio leporinus*, *Dirias albiventer*, and *Molossus obscurus*).

It is a pleasure to take this opportunity of expressing my sincere thanks to the Rev. A. Miles Moss, English Chaplain at Pará, who allowed me to live in his house (part of which soon became converted into a temporary menagerie!) during my stay on the mainland, and at whose hands I received much kindness; I am also indebted to him for a number of frogs collected from the forests in the neighbourhood of Pará. My especial thanks are also due to a Brazilian gentleman, Dr. Demetrio N. Bezerra, for his hospitality and great kindness during the five weeks which I spent as a guest at his Fazenda "Ritlandia," on Marajó Island. Dr. Bezerra gave me every possible assistance to insure the success of my visit, providing me both with horses and "vaqueiros" (cow-boys) to act as guides on many collecting trips, and also with canoes and transport for my baggage, and rendered many other services without which it would have been impossible for me to have worked in this particularly interesting locality.

## II. BATRACHIA and REPTILIA.

### 1. BUFO TYPHONIUS L. (Pl. II., Pl. III. fig. 1.)

On October 7, while collecting in the forests beyond Souza, Pará, I was called by one of the native boys, who frequently accompanied me as assistants on these occasions, to see a "Sapo" which he had found. On reaching the place, it was some time before I could distinguish anything on the forest floor besides the usual carpet of fallen leaves and an occasional Lycopod. I then observed a small toad squatting motionless among the leaves, the creature itself bearing quite an extraordinary resemblance to a leaf (Pl. II.).

The specimen has been determined as *Bufo typhonius*, but on comparison with other specimens in the British Museum it was found to be an extreme variety of the species. Normally this toad has a very warty skin, and a fringe of pointed tubercles down the sides, while on the crown there is "an enormous erect, sharp, bony ridge from the orbit to the parotoid" (5). In the

present individual the smooth skin, absence of fringe and bony ridge, and the sacral markings are all totally unlike the normal—in fact, were it not for one or two intermediate forms, no herpetologist would hesitate to describe it as a distinct species.

This toad is of interest, since it is a remarkable example of "special protective mimicry" (*vide* Poulton, 21).

The snout is sharply pointed, the back flattened, and the body depressed; running backwards from the eye along the side of the body, and extending down the leg as far as the tibio-tarsal articulation, is a well-marked ridge; not only is this ridge sharply defined, but it appears to be continuous between the side of the body and the "knee," the angular space which normally exists between these regions being occupied by a flap of skin (Pl. III. fig. 1).

Now, since the direction of light is from above, the ventral surface of the body and the fore limbs are thrown into deep shadow—this shadow having a clean sharp edge, which ends against the lateral ridge mentioned above. Thus the only conspicuous part of the animal is the flat dorsal surface of head, body, and hind limbs, which latter are usually placed in such an attitude that the feet lie close against, and partially hidden beneath, the "shins," while the "thigh" is drawn back so that the skin between the "knee" and the side of the body is stretched (see Pl. II.).

The general contour of the toad is therefore similar to that of one of the leaves amongst which it lives, the resemblance being increased by its size, its green colour, and by the presence of two small jet-black spots on the back which give the appearance of holes. There is also a faint mid-dorsal line, corresponding to the mid-rib.

Fortunately, I had my camera with me at the time the toad was discovered, and was able to obtain a series of photographs of the animal in its native habitat. It remained quite motionless while I arranged my tripod within a few inches, focussed the camera, and took several time-exposures; nor did it make any attempt to escape when it was picked up, but allowed itself to be handled without a struggle, evidently relying on the "crouching habit" to escape observation—just as a young Stone-Curlew will do under similar circumstances.

I brought the animal home and kept it alive for six weeks, hoping to learn something of its habits. During this time it was kept in a box, the bottom of which was strewn with damp leaves, and it was interesting to notice that it never made any attempt to hide beneath these, but instead always sat in full view on top of them. It took small insects—chiefly moths and flies, the latter seeming to be the favourite food. Its method of catching these was to wait until one approached within an inch radius of its mouth; when a fly ventured within this danger zone, the tongue was flicked out and in again with a motion so rapid as to be almost invisible—the victim disappearing suddenly, as if by magic.

Corresponding with its crouching habits, this little toad has but feeble powers of locomotion, its normal method being by a *series of short hops, which never much* exceed three inches. I did not once see it crawling.

2. A Brazilian "Flying Tree-Frog," *Hyla venulosa* Laur.

*Hyla venulosa*, ranging from Mexico to Paraguay, east of the Andes, is abundant in the neighbourhood of Pará, where it lives in the forests, but also occurs in the gardens and banana-groves on the outskirts of the town (Pl. IV.).

My attention was first drawn to the habits of this frog by the Rev. A. Miles Moss, with whom I was at the time staying. Mr. Moss has had a tower erected opposite the "Bosque" Gardens, Pará, which he uses as a light station for catching Lepidoptera at night, and he told me that he has several times seen these frogs—which had climbed to the platform at the top in search of insects—leap off into the darkness below; he said that he often wondered what became of them, for, although there is a sheer drop of 40 feet, he never found any shattered remains of the frogs on the ground beneath.

Having obtained some living specimens of this species, I determined to find out whether it was possible that these animals could really survive so great a fall without injury.

A preliminary experiment was made by launching one of the frogs from off the verandah of the house, whence it had a fall of about 25 feet on to the hard floor of the courtyard below. The little creature spread its arms and legs out widely as it fell, and landed the "right way up"; it appeared to be quite unhurt.

The animal was next flung high upwards, from the ground, and I was surprised and delighted to find that it invariably managed, by means of a violent wriggle, to establish itself in a definite balanced position, so that it always fell belly downwards, with its limbs stretched in a constant and characteristic attitude. Many times it was thrown in such a manner that it spun over and over on leaving the hand, but it never once failed to get into what I shall call its "gliding position" before reaching the culminating point of the trajectory, and this position, once assumed, was invariably maintained without a visible movement until the impact of landing.

At this early stage in the experiments, it was noticed that the frog appeared to fall much more slowly than might have been expected, and it was surprising to find that the impact of hitting a hard stone floor after a fall of some 35 or 40 feet did not in any way hurt the creature.

The next problem was to find a suitably high structure from which to launch the frog in order truly to test its aeronautic powers, for, since it survived the treatment just described, it seemed not improbable that it might be able to fall from any height without being damaged.

On the 22nd October I set out in the direction of Souza, a suburb of Pará, accompanied by a small Barbadian boy, named Geraldo, and taking with me some specimens of *H. venulosa*. At Souza there is a high water-tower, and up this Geraldo climbed with instructions to release the frog from the top, on a given signal, while I remained below to pick up the pieces. The tower is not less than 140 feet high, and it is situated in an open space where the ground is hard and covered at this time of year by a scanty growth of grass.

I stood near the foot of the tower, expecting the frog to fall nearly, if not quite, vertically. But on a wave from my handkerchief, I saw the little creature leap into the air, immediately spread out its limbs, and sail slowly down in fine style, passing far over my head and landing at a spot 90 feet behind me. It was quite uninjured. (There was a slight breeze blowing at the time in the same direction towards which the frog glided, but not enough, I fancy, to account for more than a few yards of lateral movement.)

The experiment was repeated, and it was found that the frog took 7½ seconds to reach the ground. On this occasion I was at the top of the tower, and was able to observe that after it had dropped the first 12 feet up or so, there was, apparently, no further acceleration in the speed of descent; for at this point a state of equilibrium is reached in which the upward pressure of the air on the ventral surface of the frog is equal to the animal's weight.

The "gliding position" is shown in text-fig. 1. The fingers and toes are spread so as to present as large a surface to the air as possible.

It has recently been suggested to me that *H. venulosa* possesses no special gliding ability—that it is able to "glide," in fact, simply by virtue of its light weight and small size, and that any frog under similar circumstances could fall from a great height uninjured.

Having made experiments in this country with specimens of the Common Frog, *Rana temporaria*, of about the same size and weight as the *H. venulosa* used in Pará, I find, quite definitely, that this is not the case. Though it has the advantage over the Brazilian frog of possessing a much greater area of web on the feet, this species falls vertically and very heavily—"like a stone"; and, turning over and over in the air, it is purely a matter of chance whether it reaches the ground on its back or its feet.

Experiments with the European Tree-Frog, *H. arborea*, were inconclusive, owing to the small size of the specimens at my disposal, but I found that they also failed to assume any constant gliding attitude, and fell vertically, frequently landing in positions other than with the feet downwards.

The gliding ability of *H. venulosa* has been described at some length, for it is of interest on account of the indirect light which

*it throws on the habits of various species of Rhacophorus, inhabiting Borneo, Java, Sumatra, and Southern India.*

As long ago as in 1869 Wallace described his famous "flying frog" (*Rhacophorus pardalis*). The Chinese workman who brought it to him assured him "that he had seen it come down, in a slanting direction, from a high tree, as if it flew" (**23**).

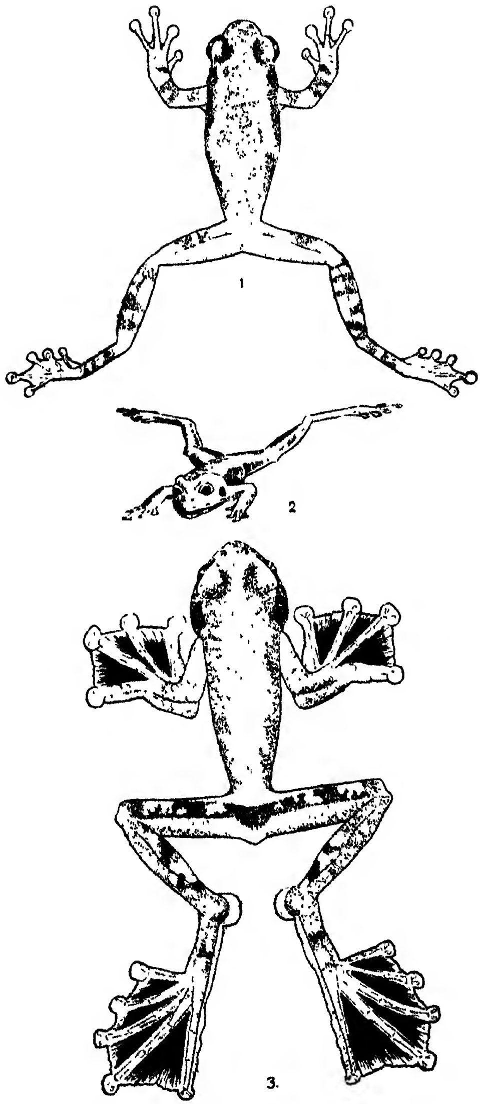
Since this date many authorities have regarded the account as being greatly exaggerated: G. A. Boulenger (**4**), referring to *R. nigropalmatus*, writes, "Beyond the statement of the Chinaman who procured Wallace his specimen, there appears to be no evidence to prove that the 'flying frog' does use its enormous feet to support it in the air, and, so far as we could see, it did not appear likely, from the condition of the web in the living animal, that their purpose was that assigned to them by the discoverer of the species." Annandale, referring to the above note, speaks of the "flabbiness" of the web—"it did not seem possible that it could be rendered sufficiently rigid, and the frog made no attempt to tauten it" (**1**). Gadow also remarks (**11**) that "Greatly exaggerated notions are . . . entertained about the parachutes," and there is certainly no doubt that many illustrations of the frog, like that in Brehm's 'Thierleben,' are grossly exaggerated.

The only piece of first-hand evidence which I am able to find with regard to the gliding of *Rhacophorus* is a very vivid account by M. O. P. Ayyanger (**2**), which is of considerable interest and is quoted here in full:—"As I appoached a big tree with my camera, my attention was suddenly drawn by a rustling noise in the leaves above, and, as I looked up, I found a beautifully coloured little animal having all the appearance of a small bird, falling from the top of the tree in a slanting direction. Its flight was curious, in as much as it did not flap its 'wings.' All the same, a sort of whir was audible as it flew slantingly. It alighted on the ground a good distance from the tree it darted from. It is a pity I failed to measure the distance travelled by the animal. It may, I think, be somewhere between thirty and forty yards. My attendant, happening to be close to where the creature alighted, ran and caught it by throwing his cloth over it. When I went to see what it was, I found to my intense surprise and delight that it was not a bird, but a gaily coloured flying tree-frog."

It seems probable that the whirring noise which Ayyanger mentions would be due to the rush of air causing the stretched webs of the feet to vibrate—like the reed of a wind instrument.

If a comparison be made between *Hyla venulosa* and *Rhacophorus nigropalmatus*, a very striking difference will be observed in the relative areas of skin available for supporting the body during a glide (text-fig. 1). The diagram of the former was taken from the actual specimen with which the experiments were made in Pará; the latter is from a specimen in the British Museum.

Text-figure 1.




1. Gliding position of *Hyla venulosa*, from above.
2. *H. venulosa* "flying."
3. *Rhacophorus nigropalmatus*.

In *R. nigropalmatus* the large hands and feet are webbed right to the base of the disc. There is a fringe of skin not only on the outside of the forearm, extending from slightly above the elbow-joint to the tip of the fifth finger, but also a narrower fringe on the outside of the second finger. A semi-lunar flap occurs on the tibio-tarsal articulation, and there is a fringe along the outside of the tarsus reaching the tip of the fifth toe; there is also a narrow fringe along the first toe.

*Hyla venulosa*, on the other hand, possesses none of these cutaneous fringes. Moreover, the fingers are only webbed at the base. The web in the feet extends almost to the discs, but the feet are small and cannot be expanded widely, as in the case of *Rhacophorus*. Yet, in spite of this deficiency in supporting area, we have seen that *H. venulosa* has, in fact, considerable gliding ability. It would not, therefore, seem improbable that some of the species of *Rhacophorus* may have the power of "flight" developed to a greater extent than has been generally supposed, and that the habit has hitherto been rather overlooked.

The question as to whether or not *Rhacophorus* can utilise the full surface of its enormous feet when in the air, by stretching the web taut, can only be determined by observing the living frog; it is to be hoped that some collector in the East, who has access to healthy living specimens, will clear up the point by performing the simple experiment of throwing one high into the air and carefully observing the manner in which it falls.

### 3. POLYCHRUS MARMORATUS L. (Pl. III. fig. 2.)

This lizard is abundant in the neighbourhood of Pará. It is decidedly arboreal in its habits (**20**), and is admirably adapted to a life among the branches.

In appearance the most striking feature is the tail, which attains an extraordinary length. Goeldi (**13**) mentions a male which had a total length of 395 mm., of which the tail accounted for 290 mm.—that is, more than two and three-quarters the combined length of head and body.

I kept living specimens for some weeks in Pará, and it is quite clear that the chief function of this organ is that of a balancing apparatus. On a previous occasion, when collecting near Morro Velho, Minas Geraes, I took a closely allied species, *P. acutirostris* *, a specimen of which was kept under observation in captivity for nearly two months.

Both species, while clambering among the branches, would frequently stand erect on their hind limbs when reaching for a branch above, and in this position the long tail hung down, enabling them to balance after the fashion of the well-known toy parrots.

The tail of *P. marmoratus* is also prehensile, and the tip is shown curled round a twig in the photograph (Pl. III. fig. 2).

* Kindly named for me by Dr. H. Gadow.

They are expert climbers, and I have frequently seen them jump for a branch that was out of reach. The hand is used as a grasping organ, the first three fingers being usually opposed to the outer two.

Like many wholly arboreal animals, their movements are slow and awkward on the ground.

As regards their food, the present species readily took moths and butterflies in captivity, but I was never able to tempt *P. acutirostris* with anything, the creature eventually dying of starvation.

*Polychrus marmoratus* is capable of changing colour to considerable extent, sometimes appearing entirely of a dark brown tint; but what may, perhaps, be regarded as the most typical coloration is a brilliant green, spotted with brown. Running diagonally down the sides of the body is a series of five or six stripes of a darker shade. This arrangement of shading looks, at a short distance, identical with that on the underside of a folded leaf, where the veins form a similar pattern of diagonal stripes. Moreover, the tail is very like a slender twig (Pl. III. fig. 2), so that the lizard is not easy to detect as it stands motionless among the branches.

### 4. Urocentron azureum L. (Pl. I.)

In the 'Catalogue of Lizards' (**6**) *Urocentron azureum* is described as being "Azure blue or olive above . . .," and Goeldi (**13**) says "A mais bella é *U. azureum* (*Doryphorus azureum* D. B., *D. brevicaudatus* Guérin), não medindo além de uns 124 mm.; é de um colorido total predominantemente ceruleo. . . ." Moreover, Daudin (**8**) and Dum. & Bibr. (**10**) both describe it as "un beau bleu," and it is represented this colour in their figures.

The lizard is rather a rarity, and I have only taken one specimen. This, however, was not blue, but a most beautiful and vivid green colour (Plate I.)*. The fact is that the green rapidly fades to a pale bluish tint in spirit. I have compared the specimen with others in the collection at the British Museum, and I find that the blue, or "museum colour," is the same in all cases, so that my specimen may be regarded as being typical in this respect and is evidently not a green variety. Instances of this kind make one realize the importance of observing the living animals in the field, besides studying their pickled bodies from a museum jar.

*Urocentron azureum* is arboreal in its habits, and on Marajó Island it lives in the large mangrove-trees which line the banks of the tidal waterways or "igarapés."

The only specimen which I saw was on a bough of one of these trees, about 25 feet from the ground. I watched it for some minutes through binoculars and found that it was busily occupied

* The precise hue is "night green," according to Robert Ridgway's 'Colour Standards and Colour Nomenclature,' Washington, D.C., 1912, pl. vi.

in catching the ants which were hurrying to and fro among the branches.

Having with me no means of obtaining the lizard, I hastily returned to the fazenda, over a mile distant, and, on arriving back at the tree half an hour later, the animal was seen to be on the same branch and was still feeding on the ants.

In case the suggestion should prove to be useful to other collectors, it may not be out of place to mention here a method which I have found invaluable for obtaining lizards belonging to various species which, for one reason or another, cannot be approached closely. For this purpose I use a large-bore revolver (·45) employing cartridges loaded with fine shot. These spread so much that the specimen is not likely to be missed, and, contrary to what would be expected, it is rare to find the specimens more than very slightly damaged.

The present specimen was obtained in this way, and is now in the British Museum.

The short tail is depressed, and is armed with whorls of sharp spines. The natives firmly believe that the lizard uses this organ to cut through the bark of trees, and they assured me in all earnestness that the little animal can fell a tree by circling round the base and gradually sawing away the wood. I have been unable to obtain any reliable evidence on the point, or to learn what habit of the lizard's is responsible for the origin of such a strange notion. On account of this belief, the species rejoices under the popular name of "serrador" (sawer) on Marajó Island.

### 5. Iguana tuberculata Laur. (Pl. V.)

The Common Iguana, so well-known throughout tropical America, is very abundant on Marajó Island, where it is called the "camaleão."

This fine lizard is, of course, essentially arboreal in its habits, but it appears that the young are by no means confined to the trees. In December I took two immature specimens on the open campo; the first of these I encountered in a place at least half a mile from the nearest isolated tree, while there was no forest within a distance of five miles in any direction—the nearest locality where adult iguanas were likely to be found being a strip of dense vegetation bordering the side of an "igarapé" (lit. canoe-path), some six miles to the south. On being approached this individual took to its heels, and I was surprised at the considerable speed with which it got over the ground, for most arboreal lizards are poor runners. The specimen measured 295 mm., of which no less than 213 mm. was occupied by the tail.

Young specimens differ markedly from the adults. The dorsal spines, so characteristic in the adult, are so small as to be scarcely visible, while the throat-pouch is but slightly developed (*vide* Pl. V.). Moreover, the colour is bright green, and the

blackish markings on the flanks and tail of the adult are represented by patches of brown madder; there is also a row of diamond-shaped brown spots along the mid-dorsal line of the body in young individuals.

6. Cyclagras gigas D. & B. (Pl. VI.)

This handsomely marked snake is fairly common on Marajó Island. It is known to the inhabitants as the "pepeua." It has the reputation of being very aquatic in its habits, but it is by no means confined to the immediate neighbourhood of water. The specimen figured (Pl. VI.) was taken in the "garden" of fazenda Ritlandia, at least three miles from the nearest lake. This individual measured two metres. They are very active and can travel over the ground at a surprising speed.

Attention is drawn to the photograph, which shows well a typical view of the campo region, Marajó Island. The trees in the background are "Tucamá" palms (*Astrocaryum tucuma* Mart.) (*vide* Pl. VI.).

7. Caiman niger Spix and C. sclerops Schneid.

In describing the Caimans of Marajó Island, it would be difficult to improve on Bates' (**3**) remark, when he says (referring to the River Solimoens) "that the waters . . . . . are as well stocked with alligators in the dry season as a ditch in England is in summer with tadpoles."

On Marajó the dry season begins early in July and lasts until the first week in January. During this period the "igarapés" and lakes contract in size considerably, so that by the end of the year great numbers of alligators are concentrated into very restricted areas. Many of the lakes which they inhabit dry up altogether, and the "jacarés" then bury themselves in the mud and lie dormant, "paralysados em uma lethargia estival que dura mezes e da qual só são libertados pelas primeiras chuvas da estação seguinte" (**14**).

Only two species are common on the island, *Caiman sclerops* and *C. niger*. *C. sclerops* has a wide distribution, extending from southern Mexico into Argentina. This beast, which is known by the native name of "Jacaré tinga," is small, and it rarely reaches more than six feet in length, though, according to Ditmars (**9**), a large example is eight feet long. On the other hand, *C. niger* attains a great length and enormous bulk, and is the largest of the New World crocodilians. Individuals of the "Jacaré assú" twelve feet long are common, while specimens of twenty feet have been reported. This species has a narrower range, being confined to the Amazon river.

The breeding season of *C. niger* is during the latter part of the dry period, and nests with eggs may be found from September to January. The nest is a large mass of decaying vegetation, about six feet across at the base, and is not unlike a swan's nest. The eggs are imbedded deep in the centre of this structure, and

number 30 to 50, though the head "vaqueiro" at Fda. "Ritlandia" assured me that he had taken as many as 70 from a nest. The period for hatching appears to be five or six weeks, the time varying with the local conditions affecting the temperature of the eggs—those in the sun hatching earlier than when the nest is surrounded by dense vegetation. Many writers state that the mother alligator remains near the nest to guard the eggs, but this is certainly not invariably the case, for though I saw several nests in December, they were quite deserted, nor did the "jacarés" come to defend their property when the nests were opened and the contents examined. I did not see the nest of *C. sclerops*, for this species breeds at the end of the wet season—in May and June (Hagmann)* (**15**) or in July (Goeldi) (**12**).

I think that the savage disposition of the Caimans is inclined to be exaggerated. My limited experience is that both the present species are great cowards, especially the "jacaré tinga," though, curiously enough, this little Caiman has the reputation of being the more "malvado e bravio." It is a common thing to ride through a lake swarming with "jacarés," either on oxen or horseback, in single file: the Caimans appear to be scared by the noise and splashing, and swim away on either side. It is preferable on these occasions to be mounted on oxen, for they are more surefooted and less liable to stick in the soft mud than horses. There is no doubt, however, that the "jacarés" are very treacherous, and I must confess that I never felt particularly at ease when riding among them in water four feet deep, though the "vaqueiros" think nothing of it, and will even enter the water on foot.

The stomach of a large individual which I examined contained entirely fish, and it is quite clear that both *C. niger* and *C. sclerops* on Marajó live almost exclusively on a diet of fish, which are remarkably plentiful in the lakes. But they will also take duck and other water birds. I once saw an enormous "jacaré assu" chasing a family of ducklings; it rushed through the water at a great speed, lashing the surface into foam with its powerful tail and snapping its huge jaws as it went. The number of wild duck that live in the groves of giant arums, *Caladium arborescens* (which commonly border the lakes), may be judged by the fact that I have seen a cowboy kill eight birds with a single 12-bore cartridge, and on the report of the gun the birds got up in thousands, flying off in a cloud that must have covered many acres. This incident is mentioned to show what a great quantity of food is available for the "jacarés," and it cannot be wondered that they thrive as they do, occurring in such numbers that they are considered a danger to the owners of the ranches.

They earn this unpopularity from the fact that they kill calves

* I am indebted to Mr. F. L. Coggin for kindly translating the German papers mentioned in this section.

when the latter come down to the pools to drink. Moreover, cattle frequently get bogged in the soft mud and aquatic plants surrounding the lakes, and their fate is then a horrible one, for they are eaten alive by the alligators. On account of this, great slaughters are organised at the end of the dry season, when the reptiles are more easily approached on account of the partial drying of the lakes. The "vaqueiros" drive the creatures to one side of their pool, and then proceed to dispatch them with axes and "terçadas" (long hunting-knives), many hundreds being killed in this way in an afternoon. Hagmann (**15**) describes an "Alligatorenschlacht" on the neighbouring island of Mexiana, where he saw, in two days, "ca. 800 Thiere von 1–4·2 m. Länge unschädlich gemacht wurden"; and in this connection Goeldi (**14**) says, "Em algumas fazendas situades á costa atlantica, entre o cabo Magoary e o rio Tartarugas, os incommodos e prejuizos causados pelos jacarés são taes que os fazendeiros são obrigados a fazer annualmente grandes caçadas onde os matam em quantidades assombrosas; para só citar um caso direi que em 1897, um fazendeiro que conheço matou, só nas suas terras, alem de 2000 jacarés!"

The flesh of "jacaré tinga" is eaten by the natives, and is said to be very good—the tail being the part used; the "jacaré assú" is considered to be unfit for food.

## III. MAMMALIA.

### 1. Chiroptera.

A small collection of Bats was made:

i. In the neighbourhood of Belem

ii. In the campo district of N.E. Marajó.

The following species were obtained:—

| | |
|---|---|
| 1. *Peronymus leucopterus* Peters. | Pará. |
| 2. *Noctilio leporinus* L. | Marajó Is. |
| 3. *Dirias albiventer* Spix. | Marajó Is. |
| 4. *Molossus obscurus* Geoff. | Marajó Is. |
| 5. *Glossophaga soricina* Pall. | Pará. |
| 6. *Carollia perspicillata* L. | Pará. |
| 7. *Eumops trumbulli* Thos. | Marajó Is. |
| 8. *Desmodus rufus* Geoff. | Pará. |

#### i. *Bats from Pará.*

Of the Bats taken in this district, *Carollia perspicillata*, *Glossophaga soricina*, and *Desmodus rotundus* were obtained from the well-known "cave of Bats" in the Bosque Gardens, Belem. The first appears to be the most abundant species in the cave, but *Glossophaga soricina* is also very common. Both species occur in such numbers that several specimens can be caught in a few minutes by sweeping an insect-net at random in the darkness, when the animals fly right into it and become entangled in the meshes.

It is well-known that the females carry their young when flying, until the latter are able to get about by themselves, and that they are able to support a heavy load in this way. On the 30th October, when sweeping for Bats, I took with a single stroke of the net a female and a young male of *C. perspicillata*. It was clear from the enlarged condition of the mammary glands of the female and the immature state of the male that this was a mother and her offspring, which she was evidently carrying in flight. Unfortunately, I omitted to weigh the specimems, but the following measurements are instructive:—

Female: length of head and body 56 mm., wing-span 316 mm.
Imm. male: ,, ,, 43 ,, ,, 218 mm.

On 28 October I took a single specimen of the Blood-sucker, *Desmodus rufus*, in the cave. This was a pregnant female. The single embryo was very large in proportion to the size of the mother, as the following figures show:

Female: length of head and body 79 mm., wing-span 417 mm.
Embryo: ,, ,, 50 ,, ,, 168 mm.

Two specimens of *Peronymus leucopterus* * were obtained, both from overhanging sandy banks (where they were found sleeping during the day), at Catú, near Belem.

### ii. *Bats from the Island of Marajó.*

With the exception of the strips of dense vegetation which line the "igarapés" and a few isolated spinneys, or "ilhas de mato" as they are appropriately called, trees are few and far between on the campo. However, in spite of this deficiency, three species of tree-living Bats are present in countless numbers, almost every available hollow tree being occupied by a colony.

*Noctilio leporinus* is perhaps the commonest species. This is a handsome bat; it is reddish-brown on the back, with a pale stripe running from the nape to the root of the tail, the fur on the throat and belly being orange in colour, while the ears and membranes are blackish-brown.

The species possesses a peculiarly powerful and unpleasant smell, which is so strong that the presence of the bats may be discovered and their exact whereabouts determined by it alone. Frequently, when riding over the campo, I have detected the smell at a distance of more than 100 yards from the nearest part of the copse which they occupied. The best way to capture the bats is to smoke them out during the daytime by burning grass or leaves in their holes.

The present species does not appear to share its diurnal hiding-places with other species; for, though I examined many trees, I never discovered either *Dirias albiventer* or *Molossus obscurus* in the same holes with *N. leporinus*.

On the other hand, *D. albiventer* and *M. obscurus* frequently

* My thanks are due to the Rev. A. Miles Moss for a specimen of this bat.

live together in the same trees. Large colonies of the latter species also live during the daytime under the tiled roofs of the buildings. The shed which I used as a photographic dark-room during my stay at Fazenda "Ritlandia" was occupied by these bats, and there was a heap of droppings several inches deep on the floor beneath their favourite roosting-place.

*Eumops trumbulli* is less common, and only one specimen of this bat was obtained—also from the roof of a house.

## 2. Hydrochœrus capybara Erxl.

Marajó Island has been well described by Dr. Goeldi (**14**) as "um verdadeiro El-Dorado" for the capybara. The same writer mentions that on one occasion, at the Cabo Magoary (in the N.E.), he saw a herd of capybaras which numbered "talvez de cincoenta, oitenta ou cem, ou mesmo mais ainda."

These great rodents, known in Brazil as "capivάras," are extremely shy, and it is only with great difficulty that they can be approached or even caught sight of. They do not appear ever to stray far from their native river or lake, and on the first sign of danger they bound off towards the water at full gallop. Sometimes when riding I have seen capybaras make off at top speed before I had got within half a mile of them.

Once in the water they can evade the keenest eyes, for they are strong swimmers, frequently diving below the surface, and reappearing at a distance, when they will hide among the aquatic vegetation with just the top of the head out of the water. Like that of the hippopotamus, the head is flattened above, and in this position it can well be mistaken for a patch of mud; moreover, the ears are small, and these as well as the eyes and nostrils, are situated high up, so that the animal can remain on the alert when it is itself almost entirely submerged.

On Marajó Island the capybaras are accused "de devastar os pastos," and are frequently hunted by the natives, who also use the flesh for food. But from all accounts it appears that their chief enemy is the jaguar. Although they live in the same lakes that are occupied by the "jacarés," it is said that the latter do not molest them. Once, however, while hunting alligators, I noticed a capybara struggling among some water-plants, and on approaching it I found a severe open wound in its side, which looked as if the "jacaré tinga," several hundred of which inhabited this particular lake, was not altogether above suspicion. The probability is that the jacarés are generally so well supplied with fish that they have no need to tackle larger quarry.

## 3. Didelphys marsupialis L.

I had not spent many days on Marajó Island before I became acquainted with the "mucúra grande," as the large opossum is called. On the 9th December, at 10 P.M., I was disturbed by a great noise outside the house—the loud cries of the "vaqueiros"

and the barking of all the dogs. On rushing out to ascertain the cause of the excitement, I saw that one of the farm buildings (all of which are raised on piles several feet from the ground) was surrounded by a number of cowboys, armed with hurricane lanterns and sticks, while the dogs were hunting about among the débris beneath the hut. Presently the yelling and barking increased, as an opossum, the cause of the disturbance, was discovered hiding in a corner; the animal was driven out and caught by a large mongrel.

Similar opossum-hunts are a common occurrence on the fazendas, for, although arboreal in its habits, the "mucúra" will travel across wide stretches of open country at night, in order to raid the poultry-yards for chickens and eggs. On account of these incursions, the "vaqueiros" never lose an opportunity of killing them; the fowls are generally the first to raise the alarm and as the raiders have little speed on the ground, they frequently pay the penalty of their thieving habits with their lives.

The breeding-season is at its height about the first week in December—that is to say, about six weeks earlier than in the case of *Didelphys virginiana*,— and most females taken late in December have young in the pouch. On 21st December a female which had been driven out of a thicket was lassoed by one of the cow-boys, and brought to me. This individual was carrying eight well-developed young. Judging by their large size, I should think that these could not have been less than seven weeks old, and yet they were still attached to the teats, which were greatly enlarged. According to Hartman (**18**) the attached stage of the pouch-young is (in the case of *D. virginiana*) certainly not less than 65 days and Meigs observed one litter which was attached for 72 to 74 days. This is mentioned because most writers underestimate the period, which is usually given as a month.

On one occasion I found a female with pouch-young occupying a dense thicket of tall bushes and "jassitára" or climbing palms (*Desmoncus*) on the campo. Near the top of this, at a height of about 18 feet, she had built a large nest of sticks, somewhat resembling in size and structure the nest of a carrion-crow.

## IV. Concluding Remarks.

In a country like Brazil, where a naturalist is confronted with animal life in such endless variety, there is a temptation for him to become simply a "collector," and to devote his time to capturing and preserving specimens rather than to observing the life-habits of the living creatures in their natural haunts.

Comparatively little has been written about the habits of Batrachians and Reptiles, and this is surprising, since there are few animals whose life-histories are more fascinating, and in no other classes, perhaps, is the close correlation between the animal's structure and its life-habits more striking. Even the

most apathetic observer must be amazed at the remarkable adaptive variation which has taken place in the order Lacertilia, while the breeding-habits of some of the frogs, as Gadow has aptly put it, "read almost like fairy tales."

It was impossible for me to remain more than a few months on the Amazon, and I regret that so short a time was available for observing and collecting: in Pará one soon realises that a lifetime of work would be necessary in order to become passably acquainted with the Batrachians and Reptiles which live in these mighty forests. I hope to be able to return on a future occasion and to visit some of the less well-known islands in the mouth of the river, especially Caviana and Mexiana, which, according to the reports of various travellers (**16**, **24**) would seem to be a veritable naturalists' paradise.

I am indebted to many persons for their help in the preparation of this paper; especially I desire to express my thanks to Mr. Oldfield Thomas for naming my Bats, and to Mr. H. W. Parker for working out my collection of Reptiles and Batrachians, for allowing me to examine specimens in the British Museum, and for his help on many occasions: and also to Miss J. B. Procter for kindly giving me access to her papers and for much valuable assistance and advice.

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## EXPLANATION OF THE PLATES.

PLATE I.

*Urocentron azureum* Linn.

PLATE II.

*Bufo typhonius* in natural environment.

PLATE III.

Fig. 1. *B. typhonius*. From life.

Fig. 2. *Polychrus marmoratus*. From a living specimen.

PLATE IV.

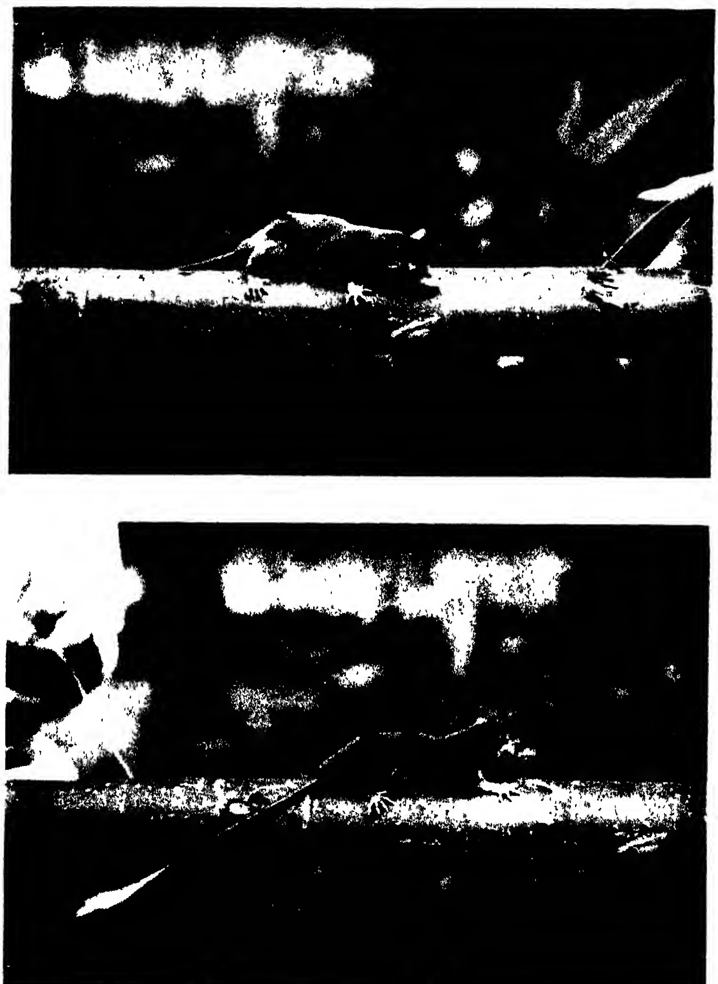
*Hyla venulosa*. Natural size.
Taken from a living specimen.

PLATE V.

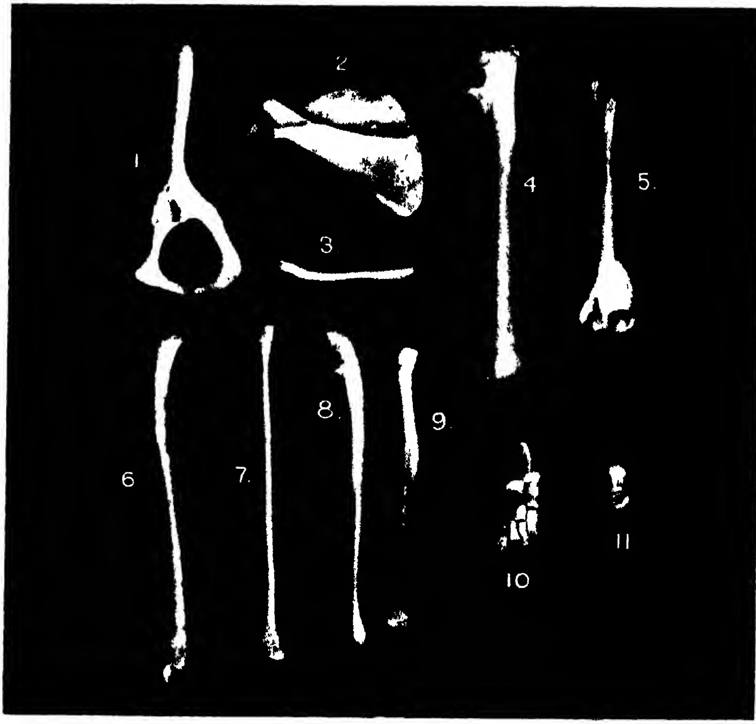
Young specimen of *Iguana tuberculata*. From life.

PLATE VI.

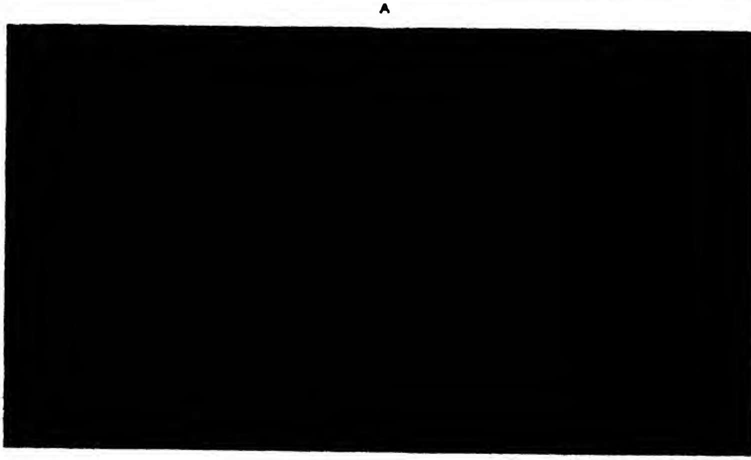
*Cyclagras gigas*.



*PTILOCERCUS LOWII.*



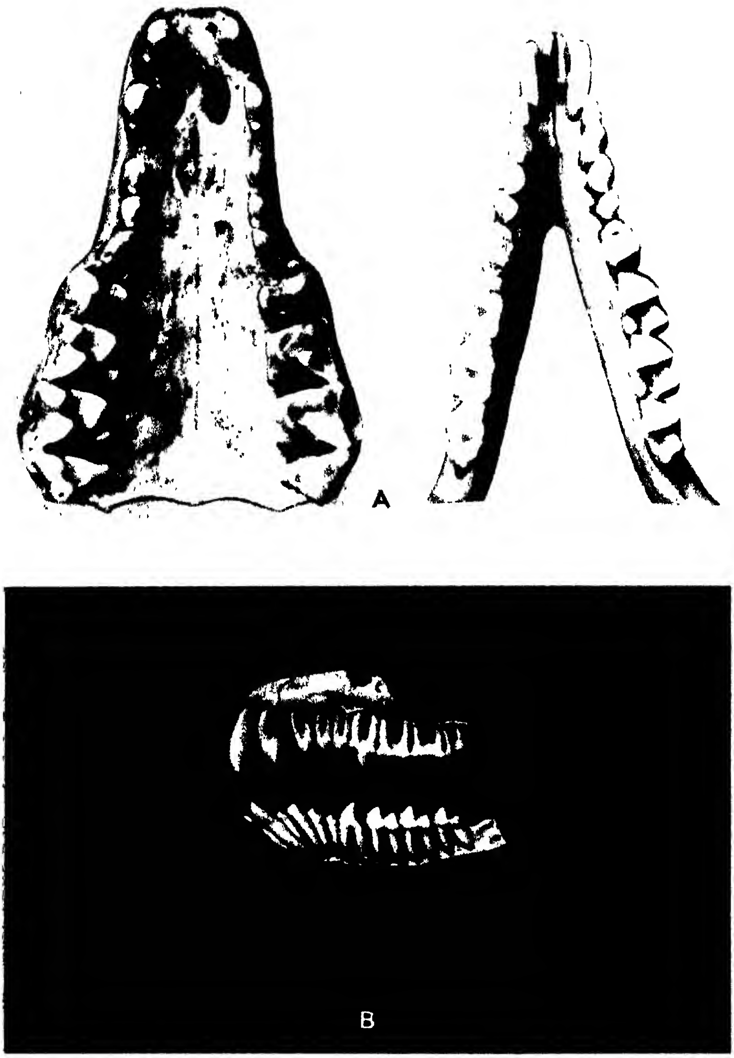

A



B

*PTILOCERCUS LOWII.*

A. LIMB-BONES. B. RADIOGRAPH OF PES AND MANUS.

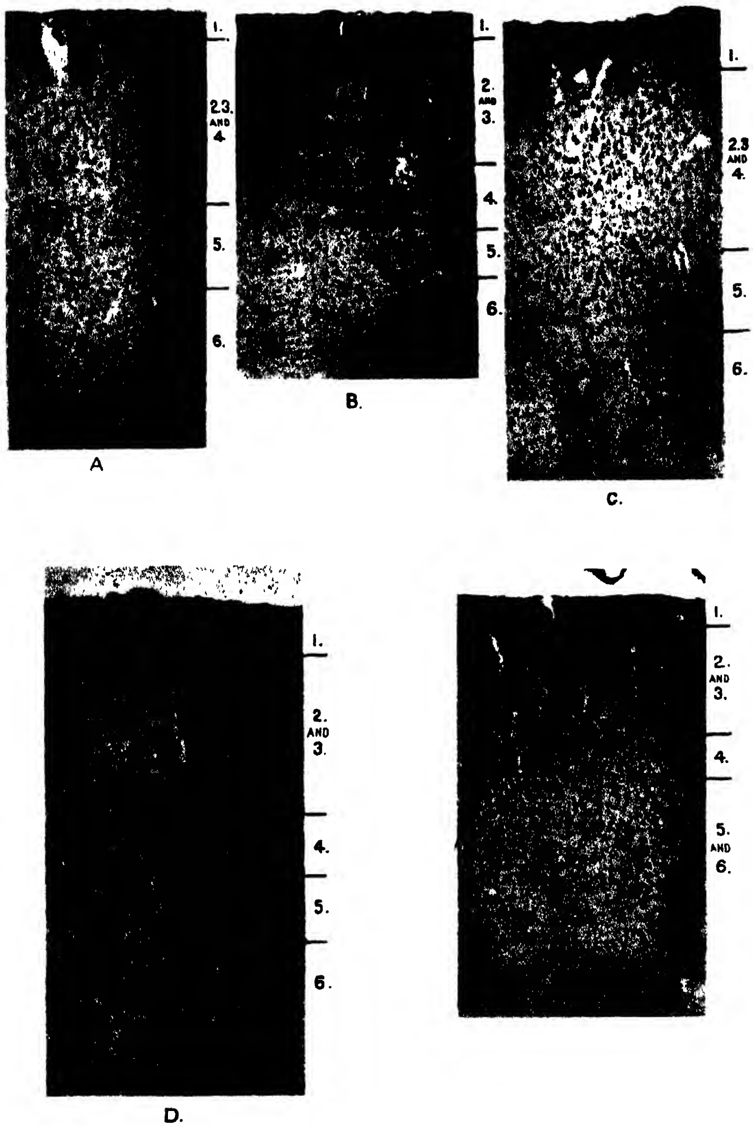



*Ptilocercus lowii*

DENTITION.

*PTILOCERCUS LOWII.*

**SKELETON**




*Ptilocercus lowii.*

Sections through Cortical areas of Cerebrum.

# 61. On the Anatomy of the Pen-tailed Tree-Shrew (*Ptilocercus lowii*). By W. E. Le Gros Clark, F.R.C.S., F.Z.S.

[Received September 6, 1926: Read November 2, 1926.]

(Plates I.–V.*; Text-figures 1–62.)

## Introduction.

In any discussion relating to the remote origin of the Primate phylum, the significance of the Tupaiidæ must inevitably be considered. For long it has been realized that the Tree-Shrews, which are usually grouped with the Insectivora, exhibit many remarkable primate features. Thus, Parker (**26**), in his classical work on the development of the skull in Mammalia, remarks on the lemuroid characters of the tupaiid skull. More recently Gregory has culled in considerable detail the osteological evidence in favour of affinities between the Tupaiidæ and Primates. Elliot Smith has adduced similar evidence in regard to the gross features of the brain. Kaudern studied the male genital organs and the abdominal musculature with the same conclusions. Wood-Jones's study of the male and female genital organs served further to emphasize these opinions. Carlsson, in 1922, produced a monograph on the Tupaiidæ and their relation to the Insectivora and the Prosimiæ, and substantiated Gregory's view that *Tupaia* is a morphologically annectant form between the true insectivores and the lemuroids. Other workers, such as van Kampen, Leche, Doran, Paulli, etc., have accumulated additional evidence, all pointing in the same direction. My own investigations into the myology and the structure of the brain and skull of *Tupaia* were also confirmatory. It is thus certain that lemuroid features are to be found in the anatomy of *Tupaia* which are extremely suggestive. But in other ways this animal demands further attention, for it is found also to present features which can only be described as primitive and metatheroid. It is, in fact, a generalized creature which, on the one hand, exhibits evidence of a lowly status in the mammalian group, and on the other, is definitely associated by a number of anatomical details with primitive forms of the Primate phylum.

The Pen-tailed Tree-Shrew, *Ptilocercus*, has not been hitherto described except for its general appearance and the general characters of its skeleton. This neglect is entirely due to the rarity of the animal. The phalanger-like appearance of the live animal as noted by Gray in his original description, and Gregory's opinion that *Ptilocercus* is somewhat more Lemur-like than *Tupaia* in its skull and dentition, sufficiently indicate the importance of making a systematic study of its anatomy. It was hoped that

* For explanation of the Plates see p. 1307.

such a study might throw additional light on the problem of the origin of the Primates.

The rarity of *Ptilocercus* is shown by the fact that Dr. Charles Hose, whose acquaintance with the mammals of Borneo as a field-naturalist is unrivalled, only met with three specimens during his long experience in Sarawak. During my three years' stay in Sarawak as a medical officer in the service of H.H. the Rajah of Sarawak, I failed to obtain any specimens. Since my return to England, however, I have had the kind co-operation of Mr. E. Banks, the Curator of the Sarawak Museum, who has unremittingly advertised in order to get a specimen. During the years 1925–26 his efforts met with some success, and, as a result, he has procured for me four male animals, together with some highly interesting photographs of the living animal. These specimens were well preserved, so that I have been enabled to carry out a detailed examination of their structure, macroscopic and microscopic, with very little difficulty. I wish here to tender my very grateful thanks to Mr. Banks for the trouble and care he has taken over this matter.

The genus *Ptilocercus* was discovered in Labuan during the voyage of H.M.S. 'Samarang,' and the species named after Sir Hugh Lowe. The animal was first described by J. E. Gray in 1848 (**11**). A distinct subspecies, *Ptilocercus lowii continentis*, was described by Oldfield Thomas in 1910 (**29**).

## Distribution.

All the specimens of the Pen-tailed Tree-Shrew of which I have any knowledge have come from Borneo, with the exception of one. The latter was caught at a point 10 miles from Kuala Lumpur, Selangor, and was described by Oldfield Thomas in 1910. He regarded it as a distinct subspecies, to be distinguished from the true Bornean *lowii* by some small points in the marking of the animal, as well as by the relative narrowness of the muzzle and palate. The skull of this specimen is preserved in the British Museum together with four other skulls of the Bornean subspecies which were obtained in the following localities:—Karimon Island, Borneo (type figured in the Voyage of H.M.S. 'Samarang'), Borneo (mainland opposite Labuan), and Labuan.

It would thus appear that *Ptilocercus* is confined to Borneo and the Malay Peninsula.

## Habits.

Little is known of the habits of this Tree-Shrew. Dr. Hose informs me that of the three specimens which he met with, two were caught in his bungalow, one by a cat. A short note (**29**) on the type-specimen of Oldfield Thomas's subspecies, *Ptilocercus lowii continentis*, yields some interesting information, for it is stated that this animal was "caught in a nest made of leaves and fibre in a tunnel two feet long in a hollow branch of a tree."

Further evidence throwing light on the habits of the animal is found in the two following accounts of the behaviour of captive specimens in Sarawak.

I am indebted to Mr. E. Banks, Curator of the Museum in Kuching, Sarawak, for the following notes on the living *Ptilocercus* :—

"The Pen-tailed Tree-Shrew is a little animal, not as big as a half-grown rat. The head is large and somewhat out of keeping with the slender body. The eyes are big and protruding. The hair is abundant, very soft, and of a rather light mouse-colour Observations on captive animals indicate that they are mainly nocturnal or, at any rate, crepuscular, and though living in a rather dark box, they only came out of their own accord in the evening and morning. During the day four (consisting of one large and active specimen and three smaller and quieter animals) slept together in a heap, mixed up and sometimes partly on top of one another, so that one could cover them all with one hand. They slept on their sides, right or left, with their snouts laid along the breast and abdomen, their hind limbs bent forward and the tail usually laid along the exposed flank with the tuft as a rule covering the snout and part of the face. This position of the tail perhaps serves to keep off mosquitoes and flies.

"These four animals lived together in harmony, but a stranger introduced was not allowed to sleep with them, and was met open-mouthed with angry squeaks, to which he replied. He died two days after being put in with the others.

"The animals slept soundly, generally near the floor of the box with a pile of wood shavings about 6 inches high on top of them. On removing the shavings one or more generally raised its snout and sniffed enquiringly, without, however, opening its eyes. On picking up one of the shrews by the tail and trying to lift it out, the others were disturbed, and usually uttered a sort of chirrup or a shrill chuckle of protest, but did nothing more. The animal seized would hold on to wood and straw with its recurved claws and was often difficult to detach. It made no attempt to bite as yet, and on being released uttered a defiant chuckle of about four notes and scurried back to its friends, there to be received with more chuckles until all was quiet. If taken by the tail and carried out of the cage to be photographed, it started to bite after many futile efforts to escape, bending its body round, grasping the base of its tail with its fore-feet and climbing up it, just as does the Tarsier.

"The bite has not the crushing power of the Tarsier nor the penetration of that of the Slow Loris, but the teeth can pierce one's finger-nails, and the claws draw blood as they scratch.

"The animal progresses on the ground by a series of hops, as does a munsang under similar conditions; the tail is held up in the air, the tuft almost vertically and the remainder inclined upwards at an angle of 30° or so. The claws are long and

curved, so that they always touch the surface on which the animal is walking. It climbs a door with ease, upwards, sideways, round the edge, and head downwards. In going up, it rests from time to time, and the tail is then laid flat against the surface, apparently offering support; coming down, the tail hangs free, away from the surface. In the evening they were given food consisting of small bananas about 2 or 3 inches long, of which they would eat a large quantity, one and a half or two apiece; seldom was there anything but the skin and ends to be found in the morning. In addition they ate somewhere about half-a-dozen or less cockroaches apiece, generally before the bananas. They did not take much notice of the cockroaches running about, and would probably have fared badly had not these insects been thrown heavily on the ground and rendered dazed before being introduced. As one opened the cage door and dropped in a handful of cockroaches, perhaps a couple of shrews would emerge slowly and edge up to the food. Then one of them, taking a cockroach in its mouth, would proceed to crunch it up, wings and all, making a noise which could be heard some distance away. On two occasions I saw a shrew pick up an insect in its hand and, sitting up a little on its haunches, supporting itself on one fore-leg, proceed to chew it up piecemeal, more fastidiously than it did when just picking one up in its mouth. The widespread fingers, particularly the pollex, seemed to get a good grip on the cockroach. It may be noted that the digits of the pes are also widely spread in a fan shape, though the hallux is not quite so widely opposed as the pollex. Drink was provided by sprinkling the animals with water on hot days; they had no objection to this form of bath beyond a lot of chuckling, and proceeded to lick the water off their fur very much as a Tarsier would. Their fur was always in excellent condition, though I never saw them cleaning it."

I have received further information from my brother, Capt. C. D. Le Gros Clark, F.Z.S., who kindly made notes for me on these animals when they were newly captured. He writes:—"The animal hates the light and, to avoid it, will curl itself up into a ball and push its head into a corner of the box. Hence the great difficulty in obtaining photographs of it. When shavings or straw were placed in their cage, within a few seconds the shrews had burrowed down underneath, and nothing was to be seen of them except perhaps the end of a tail. If several are together they will form a combined ball, each one attempting to get furthest from the light. While asleep the end of the tail covers the eyes and face, but whether to keep the light or insects away I could not say. In captivity the animals were fed on bananas and cockroaches. I never saw them eat a banana, which they appeared to do at night-time, but the sight of a cockroach aroused them to immediate frenzy. They would dash to the wires of the cage and attempt to hook the living cockroach from the fingers of the person holding it. With very quick jerky

movements the animal snatches the insect in its mouth and runs about the cage, apparently in fear of the insect being grabbed from it by another shrew. All the time it utters little high-pitched grunts, apparently in excitement or as a cat would growl when it has a bird or mouse. It holds the insect down with its claws while it crunches it up in its teeth. In a very few bites the insect has been completely swallowed. Once eaten, all excitement disappears, and (if no more insects are forthcoming) the shrew will once more disappear in the shavings or curl up in a ball."

There is a slight discrepancy in these two accounts as regards the behaviour of the animal when offered cockroaches. But it is evident that the latter account concerns animals which have been freshly captured and whose natural reactions have not as yet been impaired by the conditions of captivity.

The stomach-contents of specimen D, which was killed immediately on capture, were submitted to the British Museum for examination, and were studied there by Mr. K. G. Blair, to whom I am indebted for the following report. Referring to the stomach-contents, Mr. Blair writes:—"These would appear to consist entirely of insect-remains, but they are so fragmentary that it is difficult to recognize them. There is, however, the head and one leg of an ant, and various fragments of tegmina, wings, spiny tibiæ, an antennæ, etc., of a large Tettigoniid Grasshopper, possibly a species of *Gryllacris*. There are also fragments of at least one other species of insect that I am unable to recognize, probably Hymenopterous or Coleopterous."

The evidence at hand thus indicates the following conclusions regarding the habits of the Pen-tailed Tree-Shrew. The animal is nocturnal or crepuscular, leads an arboreal life, constructing nests in hollow branches, and lives on a mixed diet consisting of insects and fruit. This tendency to an omnivorous diet, it is interesting to note, had already been deduced by Gregory from a comparative study of the animal's dentition.

## Material.

The material upon which this study is based consists primarily of four adult male specimens of *Ptilocercus lowii* sent to me from Sarawak by Mr. Banks. Specimen A was preserved in 10 per cent. formalin, and was in excellent condition except for the brain, which was useless even for macroscopic study. This animal was systematically dissected with the help of a Leitz binocular dissecting microscope. Specimens B and D were also preserved in 10 per cent. formalin, and fortunately were in a sufficiently good state of preservation to allow a complete histological examination to be made of the brain. After removal of the brain the whole head of the animal B was decalcified and cut in serial sections in order to enable a study to be made of the structure of the skull with especial reference to

the olfactory and tympanic regions, of Jacobson's organ, of the tongue and teeth, of the orbit, and of the finer details of the facial musculature. In addition, histological preparations were made of portions of the alimentary canal, the endocrine organs, the abdominal musculature, the urogenital system, etc. Specimen C was preserved in spirit, but was found to be of little use except for the preparation of a skeleton. Both the latter specimens, however, were used to corroborate questionable details which had been brought to notice in the dissection of specimen A.

For the study of the skull and dentition, use was made of the collection of skulls in the British Museum (Natural History), and for permission to make this study I am indebted to Mr. Oldfield Thomas. I am also indebted to Mr. Martin C. Hinton, of the British Museum (Natural History), for having an excellent skeleton prepared from specimen C. I should like to acknowledge here, also, the beautiful series of photographs of a skeleton of *Ptilocercus* sent to me by Professor Gregory from the American Museum of Natural History, New York.

## MEASUREMENTS.

The four specimens of *Ptilocercus* were practically the same in weight and measurements, and a table of the average weight and principal measurements is given here.

| | |
|---|---|
| Weight | 46·4 grams. |
| Tip of nose to base of tail | 125 mm. |
| Tip of nose to inion | 45 mm. |
| Width of head measured at base of tragus. | 23 mm. |
| Brachium | 23 mm. |
| Antibrachium | 25 mm. |
| Manus | 16 mm. |
| Third digit of manus, measured from metacarpo-phalangeal joint | 9 mm. |
| Pollex | 5·5 mm. |
| Thigh | 25 mm. |
| Leg | 30 mm. |
| Pes | 26 mm. |
| Third toe | 10 mm. |
| Hallux | 6 mm. |
| Palpebral fissure | 7 mm. |
| Thoracic diameter. Dorso-ventral | 20 mm. |
| Lateral | 19 mm. |
| Tail | 177 mm. |
| Terminal hairy portion of tail | 80 mm. |
| Terminal part of tail covered with white hairs | 60 mm. |

## External Characters.

*General Form.*—This is well shown in the photographs of the living animal (Pl. I.) which were taken by Mr. Jee Koo, assistant in the Sarawak Museum, and sent to me by Mr. Banks, the Curator of this museum. It will be seen that the illustration of this animal given by Gray in his first description of the genus in 1848 and drawn from a spirit specimen is remarkably lifelike. The only point which calls for criticism is the fact that the ears are there figured as small, whereas they are really somewhat large. The animal is evenly proportioned except for the tail, which is two-fifths as long again as the body. The general appearance is very similar to that of *Marmosa*, and, indeed, the resemblance of *Ptilocercus* to small arboreal marsupials has been noted by previous authors. The limbs are of moderate length, the front pair being about three-quarters the length of the hinder.

*Pelage.*—The description originally given by Gray was as follows:—Blackish-brown, very minutely grizzled with the yellowish tips of the hairs; lips, lower part of cheeks, chin, and under surface of the body yellowish; sides of face enclosing the eyes black. Tail black; barbs white, except for a few hairs near the scaly part, which are black. The only striking feature, therefore, is the black-and-white tail, the animal being otherwise very uniformly coloured.

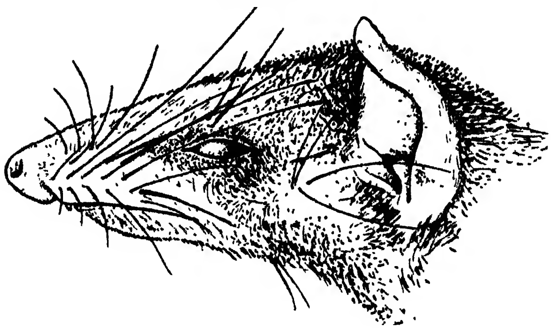
With regard to the microscopic structure of the hair of *Ptilocercus*, Mr. F. Martin Duncan, F.Z.S. (to whom I am also indebted for text-fig. 5 B), has provided me with the following note based on his own studies:—"The hairs clothing the body are very fine in texture, and have on their surface small cuticular imbricate scales of acuminate form, while the medulla is discontinuous, simple, and ovate in character. The hair from the tail-tuft is stouter than that of the body-coat, and has moderately wide, flattened, imbricate, cuticular scales and nodose medulla."

*The Head* is relatively broad, partly owing to the moderate projection of the snout and partly to the strong development of the zygomatic arches. The width is further accentuated by the thick covering of soft hair on the cheeks and frontal region. The eyes are by no means small, the orbital fissure being on the average 7 mm. in length. The eyelids show a row of fine black lashes disposed along the outer aspect of their free margin. The iris is of a brown colour, and as far as can be ascertained from preserved specimens, the pupil is round. The palpebral conjunctiva is deeply pigmented. The rhinarium is naked. The superior surface is entire and covered by small rounded nodules. The anterior surface is marked by a median sulcus, which is continued down to the free margin of the lip. On either side of this sulcus and bounded laterally by fainter vertical furrows are two surfaces covered by fine parallel grooves running transversely. The nares are comma-like slits which open laterally. The rhinarium is separated laterally from the lateral part of the upper

lip by a short furrow. The latter ends at the free margin of the lip in a notch which accommodates the apex of the prominent first upper incisor tooth.

The lips have a narrow rounded edge which is devoid of

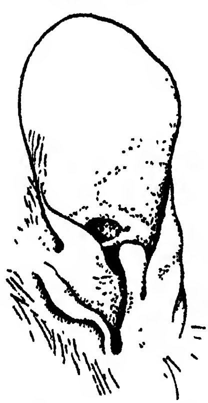
Text-figure 1.



Head of *Ptilocercus*. (× 1½.)

elaboration. The ear is large, measuring 22 mm. in length (from the apex to the incisura intertragica) and 10 mm. in breadth. As will be seen, the auricular musculature is especially well developed, and there is every indication that the organ is freely

Text-figure 2.



Ear. Left side. (× 2.)

mobile. The cranial surface of the pinna is covered with hair, but over its upper half these are so sparse and fine that they can only be detected by examination with a good lens. The meatal surface is naked. The tragus forms a thickened elongated ridge

extending forwards and dorsally, with an everted margin. The antitragus is produced into a blunt process, which projects upwards for about 4 mm. and ends in a rounded tip which comes into relation with the fossa triangularis. It is separated from the posterior margin of the pinna by a sharp cleft. Overhanging the inferior articular fossa is a conspicuous transverse ridge, the plica principalis, separating the inferior articular fossa from the fossa triangularis above. The latter is bounded dorsally by another ridge not so prominent—the antihelix. The crus helicis is well developed, and soon becomes lost in the free margin of the

Text-figure 3.

Manus. (× 3.)

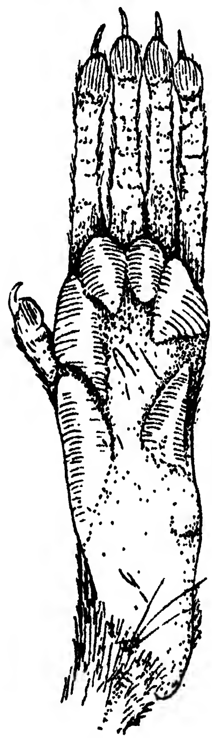
pinna when traced dorsally. In front of the crus helicis, extending on to the cheek, is a bare area reaching forward for a distance of some 5 mm.

*The Manus.*—The digital formula is $3>4>2>5>1$. The pollex is well developed, and would appear capable of a considerable degree of divergence. That such is actually the case is clearly seen by reference to the photographs of the living animal (Pl. I.). The palmar surface is unpigmented and the fine hairs covering the dorsum distal to the carpus are a dirty white colour. The palmar pads are arranged in their simplest form, the four interdigital pads, the thenar and hypothenar pads being

quite separate from each other. They are covered by fine papillary ridges, the direction of which can be seen from text-fig. 3. In addition to the rounded terminal pad of each digit covered with papillary ridges which run parallel in the axis of the digit, the palmar aspect of the phalanges are covered with small, irregular, papillated areas separated by intersecting creases.

*The Pes.*—The digital formula is $3>4>2>5>1$. The development of the hallux and the degree of divergence of which

Text-figure 4.

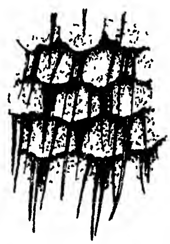


Pes. (× 3.

it is capable are to be noted, and reference should again be made to the photographs in Pl. I. As in the manus, the plantar surface is unpigmented and the dorsum distal to the tarsus is covered by short hairs of a dirty white colour. The interdigital pads are evenly arranged and distinct both from each other and from the thenar and hypothenar pads posteriorly. The pads on the digits show the same arrangement as in the manus. In both the pes and manus the claws are large, strongly curved, laterally compressed, and sharply pointed.

*The Tail* is perhaps the most conspicuous of the external characteristics of *Ptilocercus*, and, indeed, the animal owes its name to the appearance of this appendage. In specimen A the tail measured 173 mm. in length, of which the terminal 77 mm. are furnished with hairs disposed laterally in a bipenniform

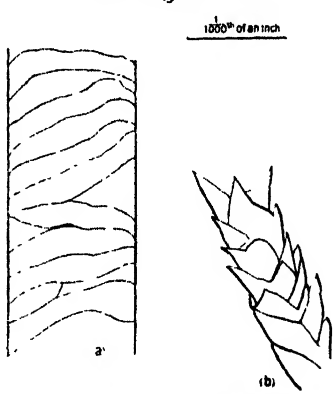
Text-figure 5 A.



The Scaly Epidermis of the Tail. (× 6.)

arrangement. For the proximal 18 mm. of this hairy portion the hairs are jet-black, and distal to this they are white. The base of the tail for some 20 mm. is covered with long hair directly continued from the trunk. This gives the appearance

Text-figure 5 B.




(*a*) Tail hair. (*b*) Body hair, showing shape and arrangement of the cuticular scales. (× 500.)

of a gradual transition from the trunk into the tail. The greater part of the tail is covered with scaly epidermis, the scales being regularly arranged in an imbricating fashion. From under cover of the distal border of each scale appear three stout bristle-like hairs, of which the central is usually the longest. This

"three-hair group" arrangement has previously been noted by de Meijere and others. The skin of the tail is deeply pigmented, except where it gives attachment to the white hairs at the end. There are no bare areas on the tail.

*Vibrissæ.*—These are very conspicuous, especially on the head. Six or seven rows of maxillary vibrissæ were counted, some reaching to a length of 30 mm. Above the middle of the eye are two or three supraorbital vibrissæ. The genal group is also well developed, and consists of about eight hairs. Two or three fine interramal vibrissæ are present 18 mm. behind the point of the chin. Mandibular vibrissæ are feebly developed, and are represented by one row of four or five short hairs.

Carpal vibrissæ, six in number, are situated on a well-marked hillock on the ulnar side of the forearm, 5 mm. proximal to the wrist.

Three somewhat inconspicuous calcaneal vibrissæ were noted projecting from a small pigmented spot on the medial side of the prominence of the heel.

### *The External Genitalia.*

No female specimen of *Ptilocercus* has as yet been obtained. The female external genitalia have, therefore, not been studied. In the male the scrotum forms a prominent spherical swelling underneath the base of the tail. I am informed by the observers quoted at the beginning of this paper on the behaviour of the live animal, that the sac forms a very conspicuous object during life. The skin of the scrotum is unpigmented and corrugated, and only sparsely covered with light yellowish hairs. It is marked by a rough median raphe which can be traced posteriorly into the anterior lip of the anal orifice. At the caudal end of the ventral surface of the scrotal sac is a slit-like aperture leading into the preputial sac, and, except for the slight raising of the margins of this aperture, the penis is not visible externally, being completely enveloped in the scrotal swelling.

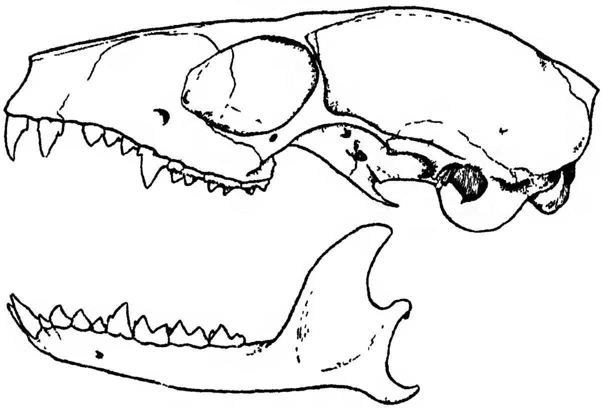
The anal orifice forms a transverse slit 3½ mm. in length with corrugated margins. The openings of the anal glands could not be detected on naked-eye examination.

## The Skull.

In general view the skull of *Ptilocercus* is evenly proportioned, with a snout of moderate length, large orbits, strongly bowed zygomatic arches, and distinct muscular markings. In the adult the cranial sutures are mostly obliterated or can only be made out with difficulty, so that it was necessary to examine the skulls of immature specimens in order to determine the sutural lines with precision. Fortunately, among the series of five skulls in the Natural History Museum at South Kensington there are two immature specimens which served this purpose.

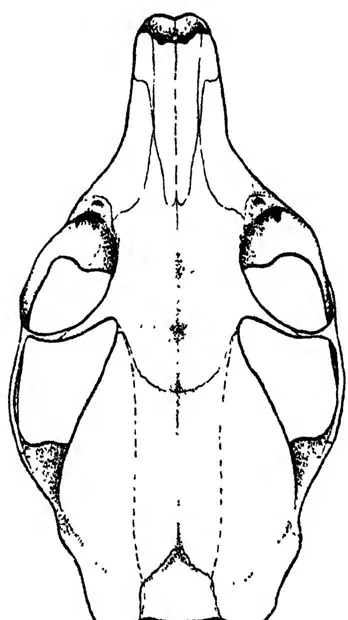
*The Frontal Bone* is single in the adult skull but double in the

Text-figure 6.



Lateral view of the Skull. (× 2.)

Text-figure 7.



Dorsal view of the Skull. (× 2.)

immature specimens. The dorsal surface shows a series of low rounded elevations corresponding to the ectoturbinal part of the nasal cavities, the olfactory bulbs, and the frontal poles of the cerebral hemispheres. The medial margins of each frontal bone diverge anteriorly to enclose the posterior extremities of the nasals, and each frontal bone forms anteriorly a sharply-pointed process which projects forwards to reach (usually) the premaxilla. Laterally, the frontal articulates with the maxilla and lachrymal, and, in the orbit, with the palatine, orbito- and alisphenoid. The coronal suture is evenly curved with a posterior convexity which corresponds to the slight depression which lies behind the elevations for the frontal poles of the cerebrum. The post-orbital processes are well developed and show a slight dorsal concavity at their base. They articulate with the malars to form slender post-orbital bars. Gregory points out that Mivart's figure (1867, p. 303) suggests that this bar is not always complete. In all the skulls which I have been able to examine (nine in number) the orbit is completely encircled by a bony ring. Under cover of the base of the post-orbital process on the orbital surface of the frontal is a venous foramen, and immediately in front of the fronto-sphenoidal suture is a small ethmoidal foramen, sometimes double. The frontal bone is sufficiently thin to allow the scrolls of the ectoturbinals to be seen through the anterior part both on its dorsal and its orbital aspect.

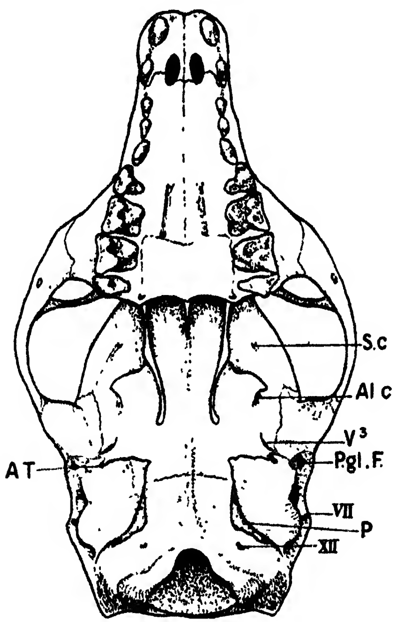
*The Nasals* are narrow strips of even width. The anterior extremities end flush with the dorsal margins of the premaxillæ, or only overhang the anterior nares to the slightest extent. The posterior extemities form blunt points articulating with the frontals at a transverse level corresponding to the anterior margins of the orbits. There is, as a rule, no articulation between the nasals and the maxillæ.

*The Premaxilla* is relatively small, and ends above in an attenuated process which projects backwards along the lateral margin of the nasal just reaching the frontal. The suture between it and the maxilla meets the alveolar margin at the posterior border of the socket for the second upper tooth. The palatal processes form the greater part of the contour of the anterior palatine foramina.

*The Maxilla* extends back to end posteriorly in a well-marked tuberosity which reaches back almost to the level of the posterior margin of the orbit. Its orbital surface is usually perforated by the apices of the roots of the last two molar teeth. The anterior opening of the infraorbital foramen lies just over the last premolar. The maxilla has a broad articulation with the frontal, and is prevented from meeting the nasal by the frontal and premaxilla. There is a broad zygomatic surface for articulation with the malar extending from the infraorbital foramen back to the interval between the 2nd and 3rd molars. The palate is relatively short and broad, and there are no palatal vacuities as in *Tupaia*.

*The Parietals* broaden out evenly when traced back from the coronal suture, and the contour of the cerebral hemispheres is distinctly marked out on the surface of the bones. Posteriorly they diverge to enclose the supra-occipital and meet the occipital crest on either side of this element. They are crossed on their dorsal aspect by the temporal ridges which run back from the frontal bone at a distance of 5–6 mm. from each other, never meeting in the sagittal plane as they do in *Tupaia*. At the posterior margin of the cerebral elevation the ridges approach each other a little more closely and then run back parallel to

Text-figure 8.




Base of Skull. (× 2.)

*S.C.* Sinus canal. *Al.C.* Alisphenoid canal. *A.T.* Auditory tube. *V*³. Foramen ovale. *P.gl.F.* Post-glenoid foramen. *P.* Os Petrosum. *VII.* Stylo-mastoid foramen. *XII.* Hypoglossal canal.

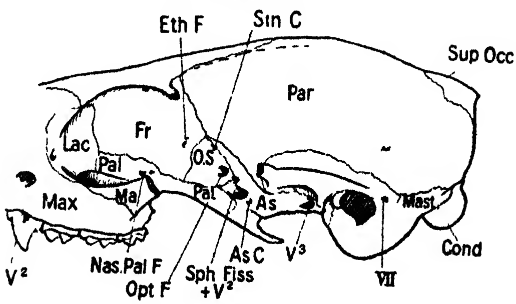
reach the occipital crest. In the orbito-temporal region the parietal articulates with the frontal, alisphenoid, and temporal, and sometimes, perhaps, with the orbito-sphenoid.

*The Lachrymal* extends well on to the face, articulating here with the maxilla. It just reaches the malar on the inferior orbital margin. In the orbit it articulates with the frontal, palatine, and maxilla.

The lachrymal foramen, which is single, lies immediately in front of the orbital margin.

*The Occipital.*—All the elements of this bone are completely anchlyosed in the adult. The supraoccipital is prolonged as a tongue-shaped plate of bone on to the dorsal surface of the cranium. Elsewhere the lambdoid suture is coincident with the occipital crest. The latter is prominent and sharp, especially laterally. At its lateral extremity it appears to bifurcate, one part becoming continuous with the supramastoid crest and one with a low ridge representing the paroccipital process. The basioccipital is smooth except for a well-marked median ridge extending forwards on to the basisphenoid. The basioccipital is completely anchylosed with the basisphenoid in the adult skull.

Text-figure 9.




Orbito-temporal region of Skull. (× 2.)

*Lac.* Lachrymal. *$V^2$.* Antorbital foramen. *Fr.* Frontal. *Pal.* Palatine. *Ma.* Malar. *Eth.F.* Ethmoidal foramen. *Nas.Pal.F.* Nasopalatine foramen. *Sin.C.* Sinus canal. *O.S.* Orbitosphenoid. *A.S.* Alisphenoid. *Opt.F.* Optic foramen. *As.C.* Alisphenoid canal. *Sph.Fiss.+ $V^2$.* Sphenoid fissure and foramen rotundum. *$V^3$.* Foramen ovale. *VII.* Stylomastoid foramen. *Sup.Occ.* Supraoccipital. *Cond.* Occipital condyle.

Paroccipital processes are represented by low ridges on the lateral margins of the exoccipitals. The hypoglossal canal is single and there is usually no posterior condylar foramen. At the lateral margin of the basioccipital, between it and the tympanic bulla, is an elongated gap representing (in part) the posterior lacerated foramen, in which the os petrosum is exposed on the basal aspect of the skull. The foramen magnum is transversely oval, measuring 6·5 mm. by 5·5 mm. The basion-opisthion plane makes an angle of 120° with the basioccipital. The condyles extend from the lateral aspect of the foramen magnum and reach forwards with an even curve close to the midline at the basion.

*The Sphenoid.*—The basisphenoid is broad, and in the adult skull is directly continuous with the basioccipital. The ali-

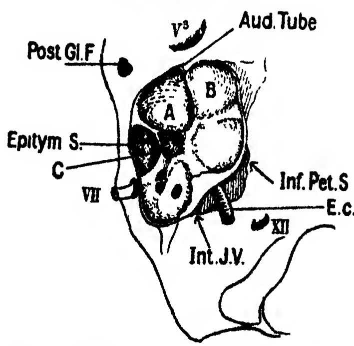
sphenoid is relatively large with a broadly convex lower surface, and extends back to the tympanic region, where it partakes in the formation of the roof of the tympanic cavity. The lateral pterygoid plates are small and everted, and are pierced by a minute alisphenoid canal at the base. The medial pterygoid processes are conspicuous, terminating in prominent hamular processes which project backwards and outwards and end in slightly bulbous extremities. A faint infratemporal crest extends forwards from the root of the zygomatic process on to the alisphenoid. The orbitosphenoid is of moderate size. The articulations of these bones on the surface of the skull can be seen from the text-figure. It should be noted that there appears to be some variation in the suture-pattern in this region of the orbit, for the alisphenoid may be separated from the frontal by a short parieto-orbitosphenoid suture.

*The Malar* is a slender bone, forming the posterior and inferior margins of the orbit. It reaches forward along the maxilla to come into contact with the lachrymal on the orbital margin. A slender frontal process completes the circuit of the orbit by articulating with the post-orbital process of the frontal. The zygomatic process extends back as far as the anterior margin of the glenoid cavity, but takes no part in the formation of the latter. The body of the malar is pierced by a foramen which transmits the malar branch of the temporo-malar nerve.

*The Temporal.*—The squamosal is small and forms an insignificant proportion of the calvarium. Anteriorly it articulates with parietal and alisphenoid. The zygomatic process is relatively short. The glenoid cavity forms an oval flattened facet with its long axis directed forwards and slightly lateralwards. It is bounded posteriorly by a well-developed postglenoid process, and immediately behind this is the post-glenoid foramen. The posterior root of the zygomatic process is continued back above the auditory meatus to end in a conspicuous supramastoid tubercle which overhangs the stylomastoid foramen and gives attachment to the anterior fibres of the sternomastoid muscle. A considerable area of the mastoid portion of the temporal is left exposed on the lateral surface of the skull behind the squamosal. The tympanic bulla is much less extensive than in *Tupaia*, and a considerable breadth of basioccipital is left between the two bullæ. Each bulla extends as far forward as the level of the post-glenoid process, and posteriorly ends in a small spur which runs back into the paroccipital ridge. Between the medial margin of the bulla and the occipital is an elongated hiatus in which the os petrosum is exposed on the base of the skull. As van Kampen has demonstrated (**18**), the bulla of *Ptilocercus* is derived from an entotympanic element as in *Tupaia*, and the tympanic ring lies free within the bulla and takes no part in the formation of the external auditory meatus. These observations I have been able amply to confirm from my own material. The interior of the bulla can readily be examined by

*removing* the thin floor of the cavity (text-fig. 10). The hypotympanic sinus is simple and undivided. Between the tympanic cavity proper and the anterior chamber of the bulla is a slight constriction where the promontory lies opposite the tympanic membrane. The foramen ovale and foramen rotundum occupy the usual position, and immediately behind the former is a small fossa marking the origin of the stapedius muscle. The sinus epitympanicus, which lodges the head of the malleus and the body of the incus, is partially separated from the rest of the tympanic cavity by a sharp incomplete septum projecting down from the roof, and is bounded posteriorly by the prominent osseous canal for the facial nerve. Medial to the sinus epitympanicus, in the roof of the bulla, are two loculi (text-fig. 10, A and C), separated by incomplete septa from each other, from the sinus epitympanicus and from the rest of the anterior chamber of

Text-figure 10.




Ventral aspect of the Tympanic Region of the Skull after the removal of the greater part of the bulla. (× 4.) A, B, C. (see text). *E.c.* Entocarotid.

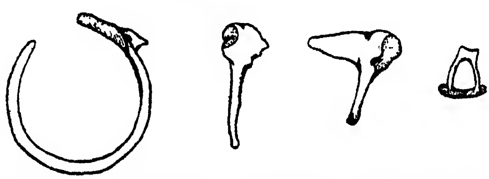
the bulla, and separated from the intracranial cavity by a thin transparent plate of bone. From the anterior of these loculi the auditory tube opens at the anterior extremity of the bulla. The promontory is a rounded swelling on the medial wall of the tympanic cavity, over the summit of which arches the osseous canal containing the entocarotid artery. At the most elevated part of the promontory, about 3 mm. from its point of entry into the bulla, the entocarotid gives off its branch, the arteria stapedia. The latter courses dorsally and posteriorly to run in an osseous canal through the stapes and thence to the roof of the tympanic cavity. The entocarotid continues in an upward and forward direction towards the opening of the auditory tube.

An examination of the intracranial aspect in specimen A, in which there was no fusion between the alisphenoid and temporal bones, showed clearly the composition of the roof of the tympanic

cavity. Thus, referring to the lettering in text-fig. 10, area A of the roof is formed by the well-developed tympanic wing of the alisphenoid, which is markedly concave on its lower aspect. Area C is formed by the os petrosum, and area B by the os bullæ (entotympanic element), covered on its upper surface by a thin plate derived from the alisphenoid. It may be noted here that a much larger proportion of the roof of the tympanic cavity is formed by the alisphenoid in *Ptilocercus* than in *Tupaia*. The endocranial features of the temporal bone will be described in connection with the intracranial cavity as a whole.

*The Auditory Ossicles.*—In order to render the account of these ossicles intelligible, they are here considered in comparison with those of *Tupaia minor* and *Lemur varius*. The malleus has a somewhat globular head. Compared with *Lemur* the head is relatively broader, and it ends anteriorly in a blunt pointed process which projects forwards. This process, however, is not equally developed in all specimens. The head is bent medially on the shaft more acutely, and does not extend upwards above the level of the articular surface. The latter is relatively more deeply

Text-figure 11.



Tympanic ring and ossicles of right ear, viewed from the lateral aspect. (× 6.)

notched and not so evenly concave. In *Tupaia minor*, on the other hand, the malleus is much less Lemur-like. Here the head is relatively small, and compressed from above downwards so that it forms a flattened plate projecting medialwards at right-angles to the upper end of the shaft. The posterior border of the head is wholly taken up by the facet for the incus, and this facet is considerably narrowed from above downwards and elongated medio-laterally. The anterior border of the head projects forwards as a point similar to that in *Ptilocercus*. The shaft of the malleus in both *Tupaia* and *Ptilocercus* is flattened from before backwards and convex medially. There is no processus muscularis to be seen in either species as in *Lemur*. The processus brevis is better marked in *Ptilocercus* than in *Tupaia minor*. In the latter it merely forms part of the rounded lateral margin of the manubrium where the latter bends medially to join the head. There is no development of a lamina on the malleus. The incus of *Ptilocercus*, compared with that of *Lemur*, shows a relatively stouter superior crus, a relatively smaller body, and a rather wider angle between the crura. The articular facet for the

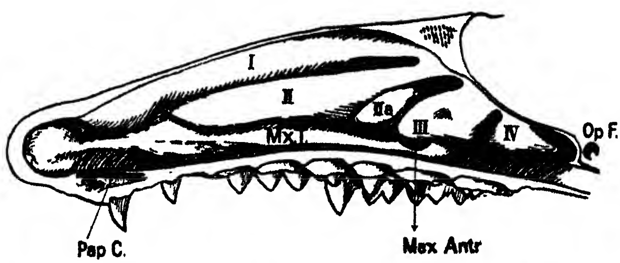
malleus is very similar. The incus of *Tupaia minor* closely resembles that of *Ptilocercus* except that the superior crus is not quite so stout, the body comes more to a point at the medial side of the articular facet, and the latter is much more concave from above downwards. The lower end of the inferior crus of the incus is slightly expanded to form a Sylvian apophysis, but there is quite definitely no separate *os orbiculare* here.

The stapes exhibits no points of difference for comment.

*The Annulus tympanicus* is an incomplete ring of bone grooved on its concave aspect by the sulcus tympanicus. Antero-superiorly it shows a small flange-like expansion, by which it is attached to the squamosal, and which is visible from the lateral aspect in the articulated skull.

*The Ethmo-turbinal System.*—The maxillo-turbinal extends from the level of the second molar tooth forwards. It is a relatively simple scroll covered by vascular mucous membrane. Anteriorly it is continued forwards by a ridge of mucous

Text-figure 12.




*I.* Naso-turbinal. *II, IIa, III, IV.* Endo-turbinals. *Pap. C.* Papillary cartilage. *Op. F.* Optic foramen. *Max.Antr.* Maxillary antrum. (× 3.)

membrane supported by the anterior end of the recurrent nasal floor cartilage and the lateral part of the alar cartilage. Just within the aperture of the nostril this ridge expands to form a rounded swelling on the floor and lateral wall of the nasal fossa covered by richly vascular mucous membrane. It is on the lower and medial aspect of this elevation that the lachrymal duct opens into the inferior meatus. The naso-turbinal extends as far forward as the level of the first incisor, the second endo-turbinal to the level of the second incisor. This turbinal possesses a secondary scroll triangular in shape from the medial aspect, which reaches to the level of the last premolar. The third endo-turbinal is somewhat quadrilateral in shape and projects downwards and forwards, reaching anteriorly as far as the level of the first molar. The fourth turbinal hangs downwards from the posterior part of the cribriform plate. Immediately above the posterior extremity of the maxillo-turbinal and below the third ethmo-turbinal is a circular orifice leading into the shallow

vertical maxillary antrum. This cavity is lined by mucous membrane embedded in which is an abundance of mucous glandular tissue. Serial sections through the nasal cavity indicate that there are two ecto-turbinals only. Herein *Ptilocercus* shows complete agreement with *Tupaia*.

*The Palatine.*—This bone forms about the posterior quarter of the bony palate, and in the suture between it and the tuberosity of the maxilla is a foramen for the posterior palatine vessels and nerves. The orbital plate of the palatine is relatively extensive, reaching from the level of the foramen rotundum posteriorly to the lachrymal in front, thus completely separating the orbital plate of the frontal from the maxilla. The middle of the palatine here is perforated by one or two nasopalatine foramina. There is thus complete agreement in the construction of the orbito-temporal region of the skull between the Tupaiidæ and the Lemurs (**33**).

*Mandible.*—The horizontal ramus is slender, ending anteriorly in a sloping symphysis 5 mm. in length. The small mental foramen is situated below the middle premolar tooth. The ascending ramus is broad and strongly built. Its lateral surface is hollowed out by the attachment of the powerful masseter. The angle of the jaw forms a curved, pointed process which projects backwards and very slightly medially. The coronoid process is large and somewhat recurved. The neck of the condyle is short and the articular surface forms a transversely oval flattened facet.

*The Intracranial Cavity.*

Anteriorly are to be seen the oval olfactory fossæ, of which the floor, the anterior wall, and the anterior part of the lateral wall are perforated by numerous small foramina for the passage of the olfactory nerve filaments. The optic foramina are well separated by the body of the presphenoid from each other, and by a relatively thick bar of bone from the combined sphenoidal fissure and foramen rotundum which lies posterolateral to it. Extending back in the midline from the level of the foramen rotundum and sphenoidal fissure to the pituitary fossa is an elevated median ridge separating on either side the broad grooves for the ophthalmic and maxillary divisions of the fifth nerve. The pituitary fossa is quite well defined though shallow, and is bounded behind by a prominent dorsum sellæ. The latter is surmounted by stout, slightly-curved posterior clinoid processes. Lateral to the dorsum sellæ are faint grooves for the accommodation of the inferior petrosal venous sinuses. The endocranial aspect of the petrous bone shows a large internal auditory meatus and a capacious parafloccular fossa. The superior border of the petrosal is prolonged medially to form a projecting spicule of bone, the petroclinoid process, ending in a free point. At the lateral extremity of the petrosphenoid suture is a small foramen through which the stapedial artery passes into the cranial cavity.

A conspicuous groove runs forwards from this foramen across the lateral wall of the cranial cavity to reach the opening of the sinus canal anteriorly. Immediately lateral to the point of entrance of the stapedial artery is the large postglenoid foramen. Communicating with this foramen are anteriorly a small groove for the meningeal vein which accompanies the stapedial artery, and posteriorly a large groove which tunnels through the petrosal to reach the groove for the lateral sinus.

The foramen ovale is a large slit-like opening leading up to which is a broad groove for the mandibular division of the fifth nerve.

*Cranial Foramina.*

*The antorbital foramen* is large and lies immediately over the last premolar tooth. It leads into a short infraorbital canal which has the usual disposition.

*The malar foramen* has already been mentioned. It is much smaller than that in *Tupaia*, and it may be double.

*The supraorbital foramen* is absent,

*The optic foramen* is conspicuous and, as usual, is situated in the orbitosphenoid. Immediately above it lies the opening of the *sinus canal.*

*The sphenoidal fissure* and the *foramen rotundum* are always confluent, but they are usually incompletely separated by a small spicule of bone projecting forward from the alisphenoid.

*The alisphenoid canal* is very small and tunnels the base of the lateral pterygoid process, opening anteriorly by a separate foramen immediately lateral to the foramen rotundum.

*The ethmoidal foramen* pierces the orbital plate of the frontal in front of the suture between it and the orbitosphenoid.

*The nasopalatine foramina,* usually two in number, pierce the middle of the orbital plate of the palatine bone.

*The foramen ovale* is large and slit-like. It lies well in front of the bulla and is not obscured by it as in *Tupaia.* There is no *foramen spinosum.*

*The post glenoid foramen* is large.

*The stylomastoid foramen* is situated on the lateral aspect of the skull immediately above and behind the auditory meatus and overhung by the supramastoid tubercle.

*The foramen lacerum posterius* is divided into two parts by an elongated gap in which the os petrosum is exposed on the base of the skull. Through the minute anterior foramen passes the inferior petrosal venous sinus. Through the posterior larger aperture the internal jugular vein and the IXth, Xth, and XIth cranial nerves leave the cranial cavity.

*The hypoglossal canal* is single and occupies the usual position. There may or may not be a post-condylar foramen.

*The carotid foramen* for the transmission of the entocarotid artery is situated at the medial margin of the bulla where the latter articulates with the petrosal and immediately in front of

the foramen for the internal jugular vein. It is not visible from the direct basal view of the skull, as it is hidden by the convex medial margin of the bulla.

*The suprasquamosal foramen* is a minute opening on the lower part of the parietal leading into a vascular canal which runs downwards and forwards to the region of the post-glenoid foramen through the squamosal.

*The anterior palatine foramen* forms an elongated oval opening the margins of which are chiefly formed by the palatal processes of the premaxillæ.

*The posterior palatine foramina* are small. In addition there is a pair of accessory palatine foramina situated in the suture between the palatines and the palatal processes of the maxillæ.

*The mental foramen* lies immediately above the middle lower premolar.

## The Dentition. (Pl. III.)

The dentition has already been considered in detail by Gregory. The present account is based on a personal study of a series of adult and immature skulls. The following is the formula which has been generally adopted for the Tupaidæ:—

$$\text{I.}\,\frac{12}{123}.\quad \text{C.}\,\frac{1}{1}.\quad \text{P.}\,\frac{234}{234}.\quad \text{M.}\,\frac{123}{123}.$$

*Permanent Dentition.*

$I^1$ is a large vertical tooth, subcaniniform and ending in a sharp point. It shows an indication of a posterior basal cusp. It is separated from its fellow by an interval of 2 mm. It has a single root.

$I^2$ is separated from $I^1$ by a short diastema. It is also a relatively large tooth, but does not project down quite as far as $I^1$. There is a small posterior basal cusp and a very faint indication of an anterior one. It has a single root, flattened from side to side and showing a longitudinal shallow groove on its lateral aspect. In his specimen Gregory noted a suggestion of an alveolus for a third incisor. In the specimens which I have examined, however, I have not been able to identify such a rudimentary socket, nor is there any indication of such a thing in the serial sections through the jaws of specimen B.

The canine is separated from the second incisor by a short diastema. It is a small tooth with a posterior basal cusp, closely resembling the premolar behind. It has two roots.

$P^2$ is very similar to the canine but slightly smaller. $P^3$ is a little larger, with the posterior basal cusp more pronounced and, in some specimens at least, a distinct protocone. This tooth is placed obliquely so that its antero-posterior axis is directed backwards and lateralwards. $P^4$ is much larger and molariform, but is dominated by a large paracone which reaches down below the level of the cusps of all the teeth except the first incisor. The

protocone is low but distinct. There is a small anterior basal cusp but no cingulum. $P^3$ and $P^4$ have three roots, two lateral and one medial.

$M^1$ shows a large protocone. The para- and metacone are equal in size. The hypocone is evident as an upgrowth from the internal cingulum, which is also present. An external cingulum is apparent, forming a parastyle and metastyle. There is no mesostyle as in *Tupaia.* The metastyle is the larger and is obliquely placed. A small protoconule is present at the anterior margin of the tooth midway between the protocone and paracone. The protoloph crest is low and insignificant.

$M^2$ is similar to $M^1$, but rather larger, with a more prominent metastyle which forms an angle projecting postero-laterally. The hypocone is not quite so large, while the protoconule is a little more distinct.

$M^3$ is a much smaller tooth. The crown is rendered triangular by an accentuation of the parastyle, disappearance of the metastyle, displacement medialwards of the metacone, and disappearance of the hypocone

The upper molars each have three roots.

$I_1$ lies in close contact with its fellow of the opposite side. It is a procumbent, styliform tooth which continues forwards the curve of the symphysis menti.

$I_2$ is stouter and a little longer than $I_1$. It is also procumbent, with a somewhat flattened lingual surface which gives it a tendency to a spatulate form.

$I_3$ is very diminutive. It has a small posterior basal cusp and is procumbent in series with the anterior incisors.

The canine is subpremolariform, with a posterior basal cusp and an internal cingulum. It has one root.

$P_2$ is similar to the canine but smaller, while $P_3$ is again rather smaller than $P_2$. $P_4$ is much larger and more molariform. It has a prominent pointed cusp showing a faint cuspule on its anterior margin and a flattened basal cusp posteriorly. It has two roots. In $M_1$ the protoconid is prominent and, with the metaconid and a smaller cusp, the paraconid, forms the primitive tritubercular pattern. The protoconid and metaconid are joined by a sharp crista obliqua which separates the trigonid from the talonid basin behind. The hypoconid and entoconid are about equally developed, and there is a suggestion of a hypoconulid.

$M_2$ is similar to $M_1$. $M_3$ is narrower and the cusps are smaller except for the hypoconulid, which is very distinct. The lower molars have two roots.

*Deciduous Teeth.*—An examination of immature specimens revealed the following points. $Id^1$ is similar in shape to the permanent tooth, but it is smaller than $Id^2$. $Id_1$ and $Id_2$ are similar to the permanent lower incisors except that $Id_2$ has a distinct posterior basal cusp.

The deciduous canines and first two premolars call for no remark. $Pd^4$ is molariform, with a well-developed parastyle and

internal cingulum, the latter showing a very small hypocone. $Pd_4$ is also molariform, with an elevated trigonid and a deep talonid basin.

*The Hyoid Apparatus.* (Text-fig. 52.)

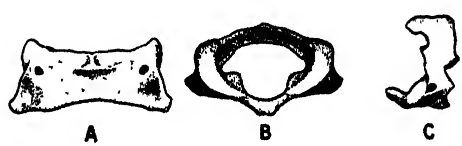
The basihyoid consists of an evenly-curved bar of bone flattened antero-posteriorly but presenting no expansions. The thyrohyal projects laterally, articulating with the basihyal by fibrous tissue. It is about the same length as the basihyal. The ceratohyal is somewhat triangular in shape with a slightly concave anterior surface. The epihyal is twice the length of the ceratohyal, and on the right side of specimen A (see text-fig. 52) this element was divided into two equal segments joined by an articulation. The stylohyal is an elongated, sabre-shaped piece of bone, broadening out posteriorly where its concave medial surface fits accurately over the convexity of the tympanic bulla. The posterior extremity of the stylohyal is attached by ligamentous tissue to the temporal immediately behind the stylomastoid foramen. Deep to and intermingling with the fibres of origin of the digastric muscle were found some muscle-fibres running from the surface of the bulla to the stylohyal, evidently representing a *M. stylomastoideus*.

## The Postcranial Skeleton (Pl. IV.).

*The Vertebræ.*

The cervical vertebræ are seven in number. The atlas is considerably wider than any of the succeeding cervical or thoracic vertebræ. The dorsal arch forms a quadrilateral plate

Text-figure 13.




A. Atlas from ventral aspect. B. Atlas from cephalic aspect. C. Axis from lateral aspect. (× 2.)

broad in the anteroposterior direction. It shows a feeble median tubercle close to its cephalic border and a well-marked ridge which runs parallel to this border on either side from the tubercle. Close to the lateral extremity of the dorsal arch is a small foramen for the suboccipital nerve. The ventral arch becomes rapidly attenuated towards the midline, where it shows a conspicuous rough tubercle for the attachment of the upper fibres of the longus colli. On the lateral part of the ventral

arch is a small foramen for the passage of the anterior primary division of the first cervical nerve. The base of the transverse process is tunnelled by the vertebrarterial foramen, dorsal to which is a very minute and presumably vascular foramen. The condylar articular surfaces are widest and furthest apart dorsally, becoming attenuated and approximated to each other ventrally. The axis has a prominent spine which projects forwards as a hook-shaped process. The body is flattened dorsoventrally and is marked on its ventral surface by a median ridge. The odontoid process juts forwards and slightly dorsally. The transverse process is very small.

The seventh cervical vertebra has a prominent spine of the thoracic type. The pleuropophysis is apparently undeveloped, and there is no vertebrarterial foramen. The remaining cervical vertebræ have low non-bifid spines. The facets of the prezygapophyses look medialwards and slightly forwards and dorsally, the postzygapophyses facing in the opposite direction. The costal elements of the transverse processes become progressively better developed from the second to the sixth vertebra, and in the latter it projects caudally ventral to the transverse process of the seventh. The laminæ of the cervical vertebræ are relatively broad and imbricated.

The spines of all the thoracic vertebræ are low and inconspicuous. The eleventh is the anticlinal vertebra. The laminæ are broad. In the lumbar vertebræ, also, the spines are poorly developed but are a little more prominent in the last two. The metapophyses are very evident, but the anapophyses are feeble. The parapophyses are slight in the first three lumbar vertebræ, but form more prominent pointed processes in the last two. The prezygapophyses face medially, and the postzygapophyses laterally.

The sacrum is formed of three fused segments, and is less than one and a half times as long as it is broad. The spines are fused to form a low median crest.

The anterior two segments articulate with the ilium.

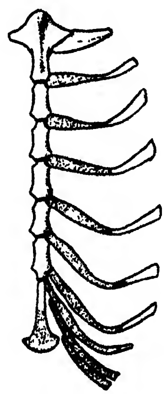
The caudal vertebræ number altogether 31. The first five show prominent flattened parapophyses, well-developed spines and metapophyses, and, with the exception of the first, have relatively large hypapophyses.

*The Sternum.*—The presternum forms a triangular flattened plate of bone. Proximally it ends in a blunt point and laterally it extends out to the first rib. Distally it narrows considerably. Along the median line of the ventral surface is a well-marked median ridge which separates on either side a somewhat concave area for the attachment of pectoralis major. No episternal ossicles were detected. The mesosternum consists of five sternebræ, each of which is slightly constricted in the middle. The metasternum is osseous in its proximal half, and distally expands to form a thin leaf-like plate of cartilage. On the deep aspect

of the sternum is a strong glistening common ligament which extends antero-posteriorly and binds the segments together.

*The Ribs* are fourteen in number. Eight or nine of these articulate directly with the sternum, three or four indirectly, and the posterior two are free or "floating ribs." As Gregory has pointed out, the ribs show a strong contrast to those of *Tupaia* in their broad and flattened shape. The vertebral ribs are conspicuous for their width and are flattened so that the external surfaces are distinctly concave. The intercostal spaces are thus left as mere slits. The costal cartilages all show a granular ossification to form a series of sternal ribs. In the case of the first rib ossification has proceeded to such a degree that there is no distinction to be seen between the vertebral and

Text-figure 14.



The Sternum and Ribs. Ventral aspect. (× 1½.)

sternal components. The sternal end of the first rib is expanded to form a flat triangular surface. In the second rib also, the ossification of the sternal element is more marked than in the more caudal ribs. It is to be noted, also, that the ossification of all the sternal ribs is greater on the ventral than the dorsal aspect, so that the costochondral junction is much more conspicuous and better defined on the dorsal aspect.

*The Upper Extremity* (Pl. II.).

*The Clavicle.*—This bone measures about 10 mm. in length. It is relatively stout and, laterally, curves in a dorsal direction.

*The Scapula.*—The cephalic and vertebral borders are gently convex, the junction between the former and the head of the scapula being marked by a shallow suprascapular notch. The axillary border is strongly everted and ends at the inferior

angle in a narrow rough area for the origin of teres major. The spine is relatively high and terminates laterally in a short flattened acromion process. The latter shows a small metacromial projection. The infraspinous fossa is larger than the supraspinous, and is further deepened by the eversion of the axillary border. The coracoid process is slender and slightly compressed in a dorsiventral direction. The glenoid cavity is markedly concave from above downwards. It forms a narrow surface extending up the lateral aspect of the base of the coracoid process, where it terminates in a distinct supraglenoid tubercle, but broadens out where it meets the axillary border.

*The Humerus.*—The articular surface of the head is evenly globular and faces in the same direction as the olecranon fossa at the distal end of the bone. The two tuberosities are well developed and of equal size. Between them passes the relatively broad bicipital groove. The prominent lateral margin of this groove is continued down into a conspicuous sharp-edged deltoid eminence. The medial margin is also very evident and presents a roughened ridge for the attachment of the teres major muscle. The shaft of the humerus is gently curved with a forward convexity exaggerated in appearance by the deltoid eminence. The lower end of the shaft is considerably broadened by the development of the supracondylar ridges. The lateral ridge is expanded to form a sharp supinator crest, which curves with a posterior convexity down to the lateral epicondyle. The lateral epicondyle is inconspicuous, but the medial epicondyle projects distally as a blunt pointed process. There is a well-marked entepicondylar foramen. The trochlear surface for the ulna has the usual form, the medial margin projecting distally beyond the level of the lateral margin. The capitellum is somewhat large relatively to the trochlea, and is separated from the latter by a distinct groove. It is not prolonged on to the posterior aspect of the lower extremity. The coronoid, radial, and olecranon fossæ are all present.

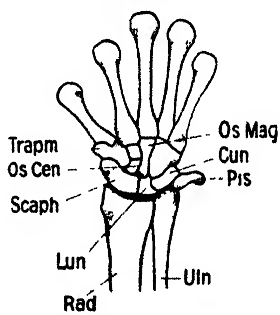
*The Radius.*—The shaft is gently curved dorsally and laterally. The proximal articular facet shows a well-marked concavity for the capitellum, and is broadly oval in shape. The bicipital tubercle is distinct, and the middle of the lateral border of the shaft is extended outwards into a sharp-edged expansion for the attachment of pronator teres. The medial border of the shaft tends to be somewhat uneven owing to irregular ossification extending into the interosseous membrane. The grooves on the dorsal aspect of the distal extremity are well marked, that for abductor pollicis longus being bounded anteriorly by a prominent tubercle. The distal articular facet is triangular and concave. The styloid process is short and blunt.

*The Ulna* is much more slender than the radius. The shaft is flattened laterally above and cylindrical below. The great sigmoid notch is narrowly constricted in the centre. The olecranon process is prominent, and, indeed, is the most strongly

developed part of the bone. The interosseous border, like that of the radius, tends to be uneven. The distal extremity is slightly expanded, flattened laterally, and produced into a short styloid process. The distal articular facet is oval in shape, oblique, and somewhat convex.

*The Carpus.*—The bones of the carpus are 9 in number, all of which are perfectly separate. The *Scaphoid* has a large and prominent tubercle. Its distal surface is deeply concave for articulation with the os centrale. The *Lunate* is less than half the size of the scaphoid. On its distal aspect it has a narrow facet for articulation with the os magnum. The *Os centrale* is approximately the same size as the lunate, its dorsal surface being considerably broader than the ventral surface It has a deep concave facet for the os magnum. The *Cuneiform* articulates directly with the ulna and, in addition, articulates also with the lunate, unciform, and pisiform. The *Pisiform* is

Text-figure 15.




Bones of the Fore-foot. Palmar aspect. (×2½.)

somewhat dumb-bell shaped, with a large proximal extremity which articulates equally with the cuneiform and ulna. The *Trapezium* has a facet for the first metacarpal which is concavo-convex and considerably expanded in a transverse direction. No groove is to be found on this bone, but there is a small tubercle on its palmar aspect. The *Trapezoid* is a small cubical bone which has the usual articulations. The *Os magnum* has an attenuated head, compressed laterally, which projects proximally to reach and articulate with the lunate. Distally it articulates with the metacarpals of the index and medius digits, but gains no contact with the metacarpal of the annularis digit. The *Hamate* is broad and triangular in shape. It articulates distally with the metacarpals of the 4th and 5th digits and by a narrow articular border with the base of the 3rd metacarpal.

*The First Metacarpal* is shorter and slightly stouter than the other metacarpals. Its base shows a concavo-convex facet for

the trapezium, and on the radial side of the base, the tubercle for the attachment of the abductor pollicis longus tendon is produced into a tongue-shaped styloid process. The other metacarpals and the phalanges offer no special features for remark.

Articulating with the palmar aspect of the trapezium is a small fusiform ossicle which evidently represents the radial sesamoid or prepollex. It gives attachment to some fibres of the thenar muscles.

*The Lower Extremity* (Pl. II.).

*The Os innominatum.*—This bone is somewhat slender and fragile in build. The obturator foramen is relatively large and almost circular in shape. In the adult the elements of this bone are completely fused together. The acetabulum is of the usual shape, though the ischial component of the articular surface is slightly expanded. The cotyloid notch is well developed. The symphysis is extremely abbreviated, measuring not more than 3 mm. in length and confined to the pubic element. The ilium is rod-shaped and prismatic in section, but it shows a tendency to a spatulate form in the slight hollowing out of the dorsal part of the lateral surface which gives attachment to the gluteus medius. The crest forms a blunt rounded point, somewhat everted, and the sacral area is small, articulating with the first two segments of the sacrum. Immediately above the acetabulum there is a conspicuous tubercle for the attachment of rectus femoris and the capsule of the hip-joint. The pubis shows a small pectineal eminence and the ischial tuberosity forms a small spur-like process. There is the slightest indication of an ischial spine. The ischio-pubic ramus bounding the obturator foramen distally is extremely slender. The ilium and ischium lie in more or less the same straight line, but the ilium and pubis are inclined to one another at an angle of about 150°.

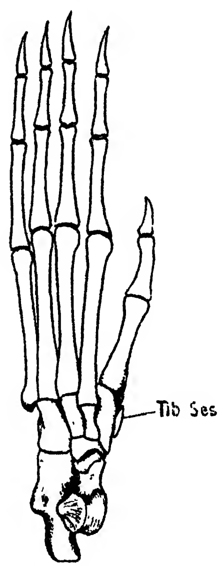
*Femur.*—The shaft of this bone is perfectly straight. The articular surface of the head is spherical and marked in the centre by a foveal pit for the ligamentum teres. The great trochanter is prominent and projects proximally not quite as far as the head. It is excavated posteriorly by a large digital fossa. The lesser trochanter is also very conspicuous. The third trochanter or gluteal tuberosity is represented by an expansion of the lateral border of the shaft immediately distal to the level of the lesser trochanter. At the distal extremity the patellar surface is broad and symmetrical. The two articular condyles are separated by a relatively broad intercondylar notch. Of the two, the medial condyle is broader and more divergent from the axis of the intercondylar notch. A pit for the origin of popliteus on the lateral epicondyle is distinct.

*The Patella* is present as a single bone which articulates in the usual way with the trochlear surface of the femur.

*The Tibia.*—The shaft is triangular in section in the upper

third and cylindrical in the lower two-thirds. The tibial crest is well developed in the upper third. The articular condyles are of approximately equal size, the medial being a little broader. They are separated by a relatively broad interarticular rough area. The surface of the condyles is directed upwards and very slightly backwards. The distal extremity of the shaft shows a conspicuous groove on its postero-medial aspect for the tendons of flexor tibialis and tibialis posticus, bounded medially by a sharp tubercle which serves to attach the strap-like ligament under which these tendons pass. The medial malleolus is a prominent, sharp-pointed process on the lateral

Text-figure 16.




Bones of the Hind-foot. Dorsal aspect. (×2½.)

aspect of which is a concave facet for articulation with the astragalus.

*The Fibula* is long and slender and completely separate from the tibia. Its proximal extremity shows a triangular expansion, concave on its medial aspect. On the upper border of this expansion is an elongated sloping facet for the tibia. The distal extremity is slightly bulbous, with an oval facet on its medial surface for articulation with the astragalus and a well-marked peroneal groove posteriorly. It forms a short, blunt styloid process below.

*The Astragalus* (Pl. II.)—The upper articular surface for the

tibia shows a shallow lateral concavity and an antero-posterior convexity. The fibular margin is elevated to a slightly higher level than the tibial. The surface is broader anteriorly. The facet on the medial side of the body for the medial malleolus is oval, concave from before backwards, and is prolonged on to the medial aspect of the neck where it becomes continuous with the sustentacular facet. The fibular facet is a little larger and is flattened and semicircular in shape. This surface is not perfectly vertical, but slopes downwards and slightly lateralwards. On the lateral aspect of the body, postero-inferiorly to the fibular facet, is a rough area for the attachment of a fasciculus of the fibular collateral ligament. The groove for the flexor fibularis tendon is well developed on the posterior surface of the astragalus, and is continued on the plantar aspect of the bone as far forward as the medial extremity of the sinus tarsi. The ectal facet is markedly concave from side to side, and is distinctly larger than the sustentacular facet. The latter forms an oblique oval surface which extends along the plantar aspect of the neck of the astragalus from the sinus tarsi to the head. The neck projects forwards and medially and terminates in a head which bears a transversely oval and forwardly directed facet for articulation with the navicular.

*The Calcaneum.*—Behind the articular surfaces, this bone is compressed laterally and it is slightly curved medially at its posterior end. The peroneal tubercle is well developed, forming a grooved shelf on which are supported the peroneal tendons, and giving origin to the accessorius muscle from its lateral margin and plantar aspect. The sustentaculum forms a prominent pointed process with a convex plantar surface, and bearing on the upper surface a facet concave laterally. The anterior part of the dorsum of the bone shows a relatively broad flat surface for the origin of the extensor brevis digitorum muscle. The posterior surface of the tuberosity is oval vertically and slightly convex. The facet for the cuboid is concave in all directions.

*The Scaphoid.*—The proximal surface of this bone is strongly concave dorsoventrally and roughly triangular in shape, the dorsolateral lip of the articular surface being produced into a definite point. There is a large triangular facet on the lateral surface for articulation with the cuboid. Of the anterior facets, that for the mesocuneiform is the largest and is markedly concave laterally. There is a flattened facet for the ectocuneiform and a slightly convex lunate facet for the entocuneiform. On the ventral aspect is a feeble tubercle for the attachment of tibialis posticus.

*The Cuboid.*—This bone shows a large convex oval facet proximally for the calcaneum, a broad dorsal surface narrowing anteriorly, and distally an oval, very slightly concave facet for the two lateral metatarsals. The groove for the peroneus

longus on the ventral aspect is well-marked. It should be noted that there is no articulation between the cuboid and the astragalus as would appear to be the case in *Tupaia*.

*Entocuneiform.*—This bone is elongated, terminating posteriorly in a point which projects back on the plantar aspect of the head of the astragalus. The proximal facet is elongated, concave, and very oblique, forming a continuous articular surface for the scaphoid and the mesocuneiform. The distal end of the medial border projects medially and distally to form a blunt flattened process. The anterior facet for the metatarsal of the hallux is roughly square and is concave dorsoventrally and convex laterally. It is disposed a little obliquely. On the medial margin of the bone is an elongated facet for the "prehallux." There is no articular facet for the second metatarsal.

*The Mesocuneiform* shows a proximal facet which forms a trochlear surface, concave dorsoventrally and convex laterally, for the scaphoid. The dorsal surface is constricted in the middle, expanding somewhat proximally and distally.

*The Ectocuneiform* is rectangular in shape and shows a well-marked facet for the second metatarsal on its medial aspect.

*The Prehallux* is a small fusiform ossicle lying along the medial margin of the entocuneiform and articulating with this bone by means of a synovial joint.

*The first metatarsal*, in being much shorter and stouter than the other metatarsals, is markedly differentiated from them. The proximal extremity has a concavo-convex facet for articulation with the entocuneiform, and on the fibular side of the base is a rounded tubercle marking the attachment of the peroneus longus tendon. The proximal phalanx of the hallux is likewise a stout bone compared with the proximal phalanges of the other digits, indicating, perhaps, some specialisation of function. The other metatarsals and phalanges show no feature worthy of special note.

*Sesamoid Bones.*—In the upper extremity, a small sesamoid is found in the origin of the supinator brevis muscle, and a pair of sesamoids in the insertions of the short flexors of the digits in connection with all the metacarpo-phalangeal joints. In the lower extremity, there is a small ossicle in the substance of the external lateral ligament of the knee-joint, and a fabella is present in each of the heads of the gastrocnemius muscle. As in the hand, a pair of sesamoids is found on the plantar aspect of each metatarso-phalangeal joint embedded in the capsule of these joints at the insertion of the short flexors. The sesamoid bones which are developed in the long flexor tendons in the palm and the sole will be described in the section dealing with the myology. The radial and tibial sesamoids found in the carpus and tarsus do not properly come into the present category, since they are not developed in connection with any tendon or ligament.

## THE BRAIN.

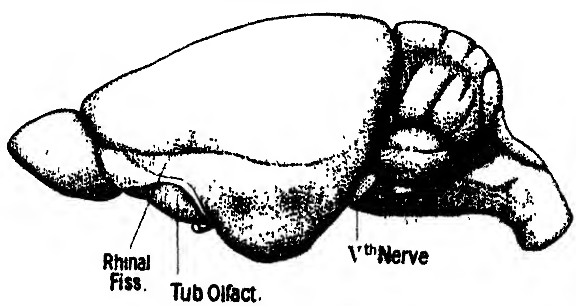
The brain of specimen C was removed entire from the skull. After an examination of its superficial aspect, the brain was cut in half. One half was used for gross dissection and the other cut in serial sections at a thickness of 15 $\mu$. Alternate sections were mounted on different slides, so that two representative series were thus obtained. One series was stained with 1 per cent. Toluidin Blue and the other with Iron Hæmatoxylin to show the myelination. The condition of the brain was not as good as could be wished for histological purposes, but the staining was sufficiently successful to allow a fairly complete study to be made of the internal structure and especially the cortical lamination.

The weight of the brain as a whole was 1·29 grams and the weight of the animal 43·5 grams. The brain weight is thus about 1/34th of the body weight, which is considerably less than the ratio in *Tupaia minor*, an animal with almost the same body weight as *Ptilocercus*.

### *The Cerebrum.*

Viewed from the lateral aspect, the hemisphere is seen to be low and elongated antero-posteriorly. The superior border is slightly arched, showing a faint depression which corresponds

Text-figure 17.

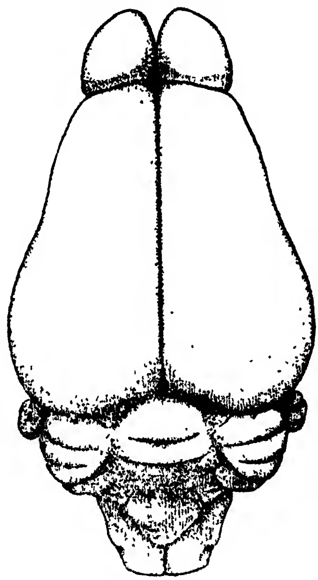



Lateral view of the Brain. (× 3.)

to the position of the bregma. The distance between the extremities of the frontal and occipital poles is 14 mm. The frontal pole overlaps the posterior third of the olfactory bulb. The occipital pole overhangs the anterior surface of the cerebellum to a small extent. The temporal pole is blunt and rounded, and shows a flattened surface where it comes into contact with the floor of the middle cranial fossa. A well-marked ectorhinal fissure runs back almost horizontally, separating the neopallium from the piriform lobe, so that the latter forms practically

the whole of the lateral surface of the temporal lobe. The fissure curves down very slightly posteriorly, and fades away before it reaches the posterior border of the hemisphere. The piriform lobe is thus exposed widely on the lateral aspect of the brain. The olfactory bulbs are large and project relatively further in advance of the frontal pole than is the case in *Tupaia*. Each bulb is about 5 mm. in antero-posterior extent and terminates in a rounded point. The lateral olfactory stria is conspicuous, and below this is the olfactory tubercle, a rounded eminence of moderate size. At the junction of the anterior and middle thirds of the rhinal fissure is a faint

Text-figure 18.



Dorsal view of the Brain. (× 3.)

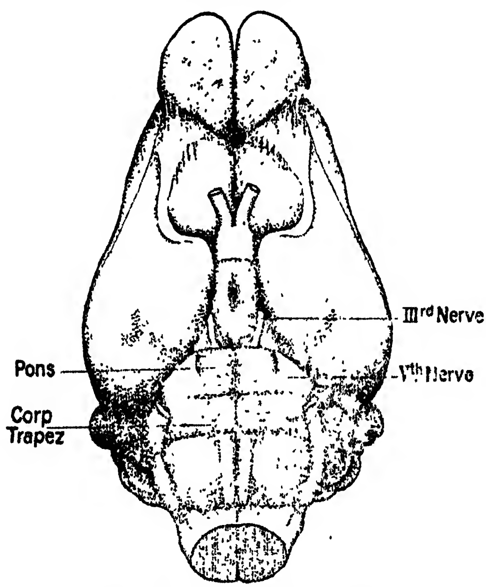
depression on the surface which accommodates a small blood-vessel.

A dorsal view shows that the hemispheres are somewhat constricted anteriorly, where they are affected by the postorbital constriction of the skull. The dorsomedial margins keep in close apposition as far back as the cerebellum, so that there is no exposure of the corpora quadrigemina from this aspect.

The basal view of the brain shows the prominent olfactory bulbs anteriorly which are almost sessile, being connected to the base of the brain by very short and thick peduncles. Behind on each side is the tuberculum olfactorium, a low,

oval eminence of grey matter measuring 7 mm. in length by 6 mm. in width. Lateral to this is the conspicuous white olfactory stria. This is broad anteriorly. Many of its fibres can be seen to terminate in the olfactory tubercle, and posteriorly it forms a narrow band which curves in rather abruptly to reach the piriform lobe. A relatively deep cleft, the arcuate fissure, separates the posterior portion of the stria from the olfactory tubercle. The piriform lobe is large, and shows on its lower surface a hollowed-out impression where it comes into contact with the superior semicircular canal. The ectorhinal fissure can be seen from this aspect anteriorly, and lateral to

Text-figure 19.




Basal view of the Brain. (× 3.)

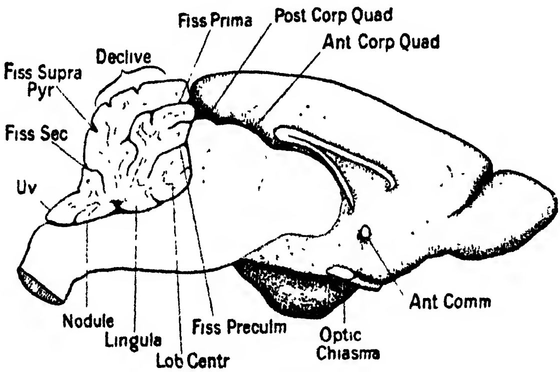
this, a very small portion of the frontal region of the neopallium. This is in contrast with the condition found in *Tupaia*, where the ectorhinal fissure is visible in the whole of its extent from the basal view.

The optic chiasma is somewhat small and behind it is the tuber cinereum bounded postero-laterally by the crura cerebri and the oculomotor nerves. The tubercle of the olfactory tract could not be identified from the surface.

The mesial aspect shows a long attenuated corpus callosum measuring 5·75 mm. in length. The proportion of the length of corpus callosum to the length of the hemisphere is thus

1 to 2·4. Caudally it is slightly thickened to form a splenium and anteriorly there is a small recurved genu. Sections indicate that the corpus callosum is relatively thinner than in *Tupaia*. Below is the psalterium curving downwards and forwards towards the ventral commissure. The latter is distinctly small. The occipital lobe is hollowed out to form two well-marked concave impressions, a large one anteriorly for the anterior corpus quadrigeminum and a smaller posterior surface for the posterior corpus quadrigeminum. These two facets are separated by a low ridge along which can be detected a very faint calcarine sulcus. Apart from the rhinal and hippocampal fissures this is the only indication of cortical sulci to be found in the brain of *Ptilocercus* either macroscopically or microscopically. The contact between the posterior corpus quadrigeminum and the occipital lobe indicates that the former body is much

Text-figure 20.



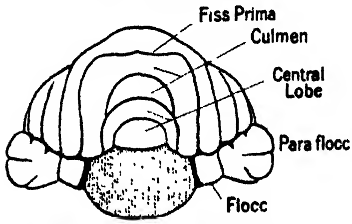

Mesial view of the Brain sectioned in the sagittal plane. (× 3.)

better developed than in *Tupaia*, for in the brain of this animal the posterior corpus quadrigeminum is separated from the occipital lobe by a considerable interval where the anterior surface of the cerebellum lies in contact with the anterior corpus quadrigeminum. Bounding the choroidal fissure can be seen the sharply defined fimbria, and caudal to this a relatively broad band of inverted hippocampus. The latter narrows rapidly above under the splenium of the corpus callosum, and below it expands to form an evenly rounded hippocampal tubercle. Behind the hippocampus is the broad dentate gyrus, relatively rather broader than it is in *Tupaia*. Separating it from the adjacent cortex is the hippocampal fissure. Above, the hippocampal formation turns directly on to the dorsal surface of the corpus callosum forming a small subsplenial flexure. Histologically, the hippocampal formation can be traced along

the dorsal aspect of the corpus callosum as the indusium as far as the genu, where it turns down to run into the gray matter of the septum pellucidum.

*The Cerebellum.*—The cerebellum of *Ptilocercus* is definitely less elaborated than that of *Tupaia*. A sagittal section (text-fig. 20) shows the division of the cerebellum into three main lobes,

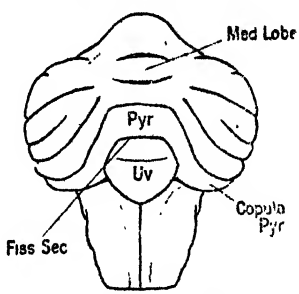
Text-figure 21 A.




Anterior view of Cerebellum. (× 3)

anterior, middle, and posterior, by two main fissures, the fissura prima and the fissura secunda. The former is a broad U-shaped sulcus which dips down to a considerable depth. Below this fissure, the anterior lobe is divided by the fissura preculminis into the culmen and the lobus centralis. Each of these lobules is again subdivided on the surface into two folia by short sulci which run

Text-figure 21 B.



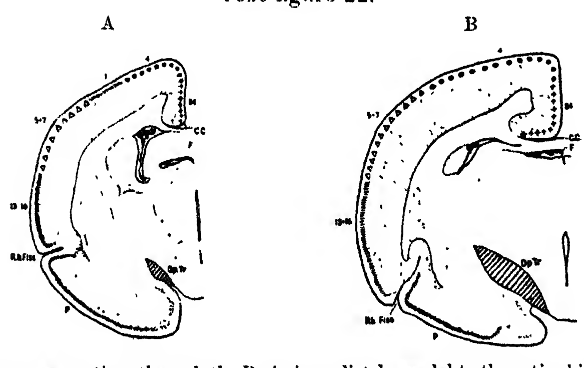

Posterior view of Cerebellum. (× 3.)

into each other below. The small lingula is hidden from view on the anterior aspect, but can be seen in the sagittal section. Behind the fissura prima is the middle lobe, which is continued laterally into the two lateral lobes. The median lobe is crossed by two short sulci which do not become continuous with the sulci of the lateral lobes. The lateral lobes are separated from the

median lobe by a shallow constriction. Each is divided into a series of folia which can be grouped into areas corresponding to those designated A, B, and C by Elliot Smith in his monograph on the morphology of the mammalian brain. Area A consists of one folium, area B is divided into two folia, and area C into three. Immediately posterior to the median lobe is the pyramid, continued laterally by a simple unfissured copula pyramidis into the paraflocculus. The latter forms a conspicuous lobule subdivided into five folia and lying in the floccular fossa of the petrosal bone in the undissected head. Behind the pyramid is the fissura secunda and behind this again, the uvula. The latter forms a tongue-shaped projection covering over the posterior medullary velum of the fourth ventricle. It is subdivided by a shallow, incomplete transverse sulcus. The nodule is hidden from surface view by the uvula, but can be seen in section. The small flocculus lies under the base of the paraflocculus. It is to be noted that the anterior surface of the cerebellum is prevented from coming in contact with the anterior corpus quadrigeminum by the dorsal extension of the posterior colliculus.

*The Mid- and Hind-brains.*—The anterior colliculi are hemispherical bodies measuring 3 mm. in diameter. The posterior colliculi, rather paler in colour, form transverse ridges measuring

Text-figure 22.




Transverse sections through the Brain immediately caudal to the optic chiasma of A. *Ptilocercus* and B. *Tupaia minor*. (× 4.)

*C.C.* Corpus callosum. *F.* Fornix. *Rh.Fiss.* Ectorhinal fissure. *P.* Piriform lobe. *Op.Tr.* Optic tract. The figures refer to Brodmann's cortical types which are mapped out on these sections.

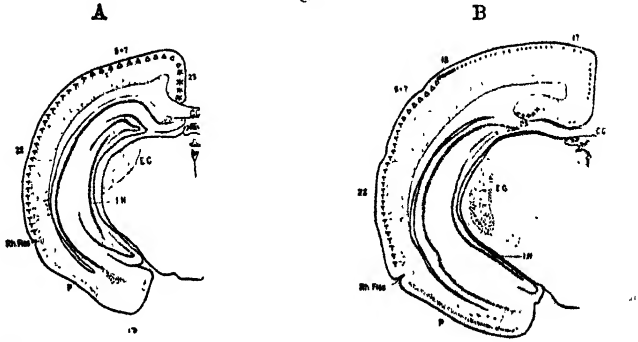
3·75 mm. laterally and 1·75 mm. antero-posteriorly. The anterior colliculi are thus much smaller relatively to the posterior than is the case in *Tupaia*. This is more clearly to be seen by reference to the vertical extent of the bodies as shown in the sagittal section (text-fig. 20). The lateral geniculate body is a low

rounded eminence on the caudal extremity of the optic thalamus, very faintly raised above the surface. The medial geniculate body, on the contrary, forms a very prominent brown tubercle measuring 2·25 mm. in diameter and situated on the side of the midbrain antero-lateral to the posterior colliculus.

The ventral aspect of the medulla shows a narrow pons, 2 mm. in width, and behind this, the corpus trapezoideum is exposed to view. The attenuated pyramidal tracts are faintly demarcated on the surface. The trigeminal nerve emerging from the lateral part of the pons is conspicuous for its size, and posteriorly are to be seen the seventh and eighth cranial nerves.

*The Internal Structure of the Brain.*—Except for the cortical lamination, the details of the internal structure, which appear to correspond in every way to what might be expected in a generalised mammalian brain, do not call for description here. It may be noted that the composition of the lateral geniculate body

Text-figure 23.




Transverse sections through the Brain immediately in front of the caudal extremity of the corpus callosum of A. *Ptilocercus* and B. *Tupaia minor*. (× 4.)
*E.G.* External geniculate body. *I.H.* Inverted hippocampus. Other references as in the previous figure.

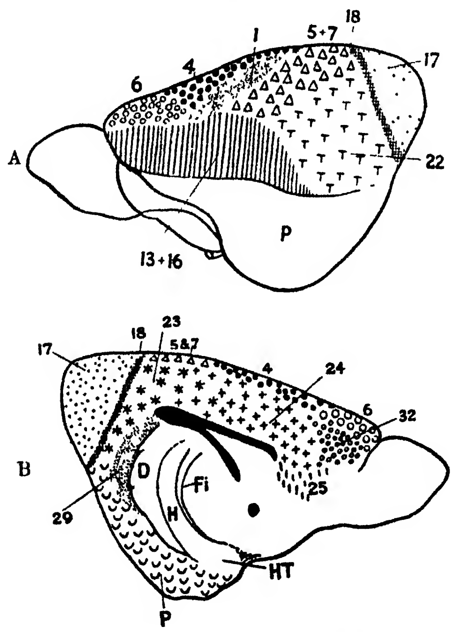
closely resembles that of *Tupaia* which has been described in detail by Woollard, but its structure is clearly more simple. The oculomotor nucleus, likewise, is not so elaborate, and no medianly placed groups of large ganglion cells are present. The cochlear nuclei of the eighth nerve are well developed.

*The Cortical Lamination Pattern* (see Pl. V.).

A study of the associated series of sections through the cerebrum stained to show the cytoarchitecture and the myeloarchitecture enabled a map of the cortical areas to be made as shown in text-fig. 24, In general, the cortex of the neopallium is relatively less thick and not so rich in cells as in the case of *Tupaia*. For

purposes of the present description, a few representative sections may be briefly described in order to point out the localisation of the cortical areas and their distinctive features. In each series, the cerebral hemisphere, from frontal to occipital pole, involved 192 sections. It will be convenient to take every 24th section for description, and thus divide up the length of the hemisphere into eight parts.

Text-figure 24.




A. Lateral, and B. Mesial aspects of the cerebral hemisphere on which the cortical areas have been mapped out. The figures refer to Broadmann's cortical types.

1. Post-central. 4. Betz cell area. 5, 7. Parietal. 6. Frontal. 17. Striate. 18. Peristriate. 22. Temporal. 13–16. Insular. 23, 24, & 32. Cingular. 25. Subgenual. 29. Retrosplenial. *P*. Piriform lobe. *D*. Dentate gyrus. *H*. Inverted hippocampus. *H.T.* Hippocampal tubercle. *F*. Fimbria.

*Section* 24 of the cortical series. In this section, the frontal area appears, extending from the medial border about half-way over the lateral surface and for a short distance down on the mesial surface. The lamina zonalis is of medium thickness and the pyramidal layer is also of moderate width, though containing a fair abundance of regularly arranged pyramidal cells. The inner granular layer is feebly developed, though it is not possible to state that it is entirely absent. The

lamina ganglionaris contains many medium or rather large pyramidal cells grouped in a regular layer some six cells deep on the average. The lamina multiformis is irregular, relatively deep and tends to fade gradually into the subjacent medullary substance. Below this area on the mesial surface is a cortical type in which the lamina zonalis is thicker, the pyramidal layer narrow the inner granule-layer absent, and the cells of the lamina ganglionaris smaller than in the frontal area. This area is clearly the anterior extension of the cingular area, and possibly corresponds to the *area cingularis anterior dorsalis* of Brodmann. It extends ventrally as far as the olfactory peduncle. On the lateral surface, lateral to the frontal area, is another type of cortex. Here, the lamina zonalis is of the same thickness, but the pyramidal layer contains not so many cells and the latter are less regularly arranged than in the frontal area. The inner granule-layer, moreover, is somewhat better developed though diffuse and there is an absence of large or medium-sized cells in the infragranular layers. The lamina ganglionaris and multiformis are imperfectly differentiated from each other. The lamination of this region of cortex is on the whole poorly marked, so that it is not easy to define the limits of each cell-layer. This area is found on tracing through the sections to be the frontal extension of the insular area of the cortex.

*Section* 48. In this section, the motor area, or the *area giganto-pyramidalis* appears. A close study of the series indicates that it first appears in about the 38th section, but the boundary between it and the frontal area is by no means sharp. In the section under discussion, the motor cortex is found at the dorso medial border of the hemisphere, extending for a very short distance on the mesial surface and on the lateral surface. The pyramidal layer here is relatively narrow, and the inner granule-layer poorly developed though it can be identified. The characteristic feature is the presence of the large Betz cells in the lamina ganglionaris. These cells show a multilaminar arrangement. On the mesial surface of the hemisphere, below the motor area, is a type of cortex which much resembles the cingular cortex described in the previous section except that the lamina ganglionaris is not so well developed and contains smaller cells, and the inner granule-layer shows a tendency to appear. This would appear to correspond to Brodmann's type 24, *area cingularis anterior ventralis.* It extends down to the corpus callosum, and, in front of this structure, meets the *area subgenualis*, an area in which there is very imperfect differentiation of the cell laminæ. On the lateral surface, lateral to the motor area, is a short extent of cortex which is of the postcentral type, or rather a transition between this and the motor area. The cortex here is relatively thick, the inner granule-layer is better developed, and the lamina ganglionaris is less densely packed with cells. Lateral, again, and occupying about the lateral third of this surface, is the insular area. It shows the same characters as in the previous section, and the

inner granule-layer is moderately developed. There is also a paucity of medium and large cells in the lamina ganglionaris. In fact, the infragranular layers give the appearance of being somewhat empty.

*Section* 72. The Betz cell area is again evident in this section and rather closely confined to the dorso-medial border of the cerebral hemisphere. The cingular area is found on the mesial surface and shows an absence of an inner granule-layer. The postcentral area, which had begun to appear in the previous section, has now reached its characteristic development. The lamina zonalis is slightly thickened, the pyramidal layer is broad and contains many regularly arranged small and medium-sized pyramids, and the inner granule-layer is well developed, contrasting with the areas already described. The lamina ganglionaris, which is clearly differentiated from the lamina multiformis, contains a number of relatively large pyramidal cells which, however, are not grouped together as in the Betz cell area Lateral to this again, is the insular area.

*Section* 96. This section lies midway between the frontal and occipital poles of the cerebral hemisphere. The area giganto pyramidalis has not appreciably altered its position. Laterally it is succeeded by a narrow band of postcentral cortex and then by the first appearance of the parietal area. The cortex of this area shows a deep pyramidal layer, a conspicuous inner granule-layer, and a relatively thick lamina zonalis. The pyramid cells of the lamina ganglionaris are medium-sized or rather small. The cells forming the lamina multiformis tend to arrange themselves in vertical rows. The insular area, which still intervenes between the parietal area and the ectorhinal fissure, shows its usual features. The infragranular layers are broader and contain more scattered cells. The cingular area has not changed, except that maybe the inner granule-layer is feebly represented.

*Section* 120. The Betz cell area has now disappeared. The cingular and parietal areas show no change except that the latter occupies a greater part of the cortical section, extending over the dorso-medial border on to the dorsal part of the mesial surface The insular area has disappeared and is replaced by the temporal cortex. This cortex is singularly lacking in distinctive features, so that it is difficult to assign a definite boundary between it and the adjacent parietal area. As a result of intensive study however, it is believed that the temporal area as mapped out in text-fig. 24 is tolerably correct. The lamina zonalis is of moderate width. The external granular layer is rather more distinct than elsewhere. The pyramidal layer is well developed but rather narrower than in the parietal area. The inner granular lamina is conspicuous and contains many small cells fairly closely packed together. The infragranular layers are relatively broad but not very thickly crowded with cells, and the latter are on the average somewhat small. The whole cortex is wide, but narrows as it approaches the piriform lobe. Although minute differences

can be detected in different parts of the temporal area, these are not considered to be sufficiently definite or sharply limited to justify any subdivision of this area.

*Section* 144. In this section, the lateral surface of the hemisphere is still occupied by the parietal and temporal areas, but the latter now extends considerably more dorsally. At the dorso-medial border, the visual cortex or *area striata* is just beginning to appear. Below this on the medial surface is the cingular area in which a definite granular layer has now appeared. This region evidently corresponds to Type 23 of Brodmann, the *area cingularis posterior*. This section lies behind the level of the corpus callosum, and the cingular area passes into a narrow band of cortex whose structure indicates that it belongs to the *area retrosplenialis*. The appearance of this cortex is very characteristic. Deep to the plexiform layer are crowded together masses of small cells, which, it seems, are derived from a local expansion and hypertrophy of the outer granule-layer, but the inner granule-layer also seems to take a part in the formation of this cell-band. It appears that layer III is absent. The infragranular laminæ are represented by very few scattered cells of medium size. By a very narrow band of presubicular cortex, the retrosplenial area passes into the subicular area and thus becomes continuous with the cortex Ammonis. The presubicular and subicular areas show the usual structure which has been described in detail by many authors. It may be noted here that these areas are quite attenuated.

*Section* 168. In this section the striate cortex occupies the greater part of the lateral and medial surfaces of the hemisphere. A striking feature is the lack of differentiation of this type of cortex, especially if comparison is made with the striate cortex of *Tupaia*. In the latter, the lamination is so remarkably developed that it is the simplest matter to map out the striate area in the brain of this animal with the greatest precision by the examination of Toluidin-Blue stained sections with a hand-lens or even with the naked eye. In *Ptilocercus*, on the contrary, the delimitation of this area requires a very close study of individual sections under different magnifications, and even then it is felt that the map represents the extent of the striate area approximately only. The boundary between the striate and cingular areas is clear enough, but there is considerable difficulty in defining the line of junction of the striate area with the parietal and temporal areas.

The striate cortex is somewhat narrow as a whole. The lamina zonalis is narrow and the lamina pyramidalis is also relatively attenuated. The inner granule-layer is moderately developed and not nearly so conspicuous as it is generally found to be in the visuosensory cortex. This layer is directly continuous with the pyramidal layer without the intervention of any clear zone. The infragranular laminæ are relatively narrow. The lamina ganglionaris contains groups of medium-sized pyramids which

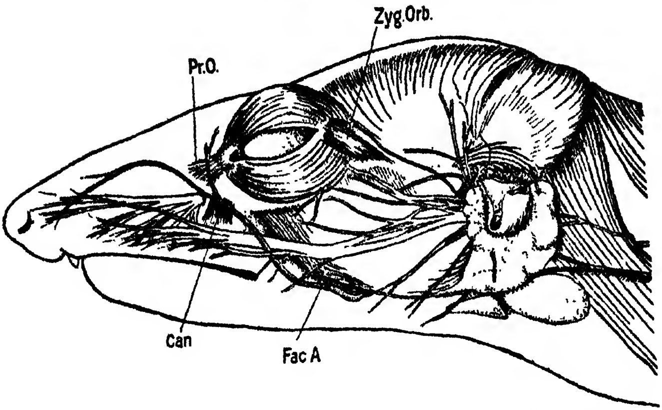
stain well, but there is an almost complete absence of the large Meynert's cells such as are found in the IVth and Vth layers in *Tupaia*. It is possible that the lack of these characteristic cells may be associated with a nocturnal type of vision, for Woollard also notes the paucity of these cells in the nocturnal *Tarsius*. The lamina multiformis contains relatively few cells which tend to arrange themselves in horizontal rows. In the myelin stained sections, a very faint suggestion of a stria of Gennari could be detected in the visual area, running through the inner granule lamina. The striate cortex of *Ptilocercus*, therefore, corresponds to the unistriate type of Brodmann such as is found in primitive mammals generally, but it is a very simple representative of this type. Surrounding this area is a narrow and ill-defined band of cortex in which the pyramidal layer is rather better and the inner granule-layer rather less developed. This may be designated the peristriate cortex, corresponding to type 18 of Brodmann. At the lower part of the section are to be seen small portions of the granular type of cingular cortex and the posterior extremity of the piriform lobe.

*General Survey of the Cortical Areas.*

The attenuated frontal pole of the hemisphere is occupied by a relatively agranular frontal area. The area gigantopyramidalis for the most part stretches along the dorso-medial margin of the hemisphere, extending a little laterally anteriorly. The insular area is relatively large. The cingular areas are well developed and form a relatively broad band occupying the greater part of the mesial surface dorsal to the corpus callosum. The anterior part is relatively agranular, and the posterior part is more distinctly granular. This broad area contrasts strikingly with the condition in *Tupaia*, where the area is constricted and in one place buried from the surface on the dorsal aspect of the corpus callosum by the pressure of the extensive striate cortex. This state of affairs is well illustrated by the diagram of a transverse section through the caudal extremity of the corpus callosum in *Tupaia minor* (text-fig. 23 B). The temporal area appears to be relatively extensive, and perhaps this is to be correlated with the elaboration of the auditory apparatus. Little stress, however. can be laid on this because of the difficulty of determining the limits of this area with precision. The striate area is of limited extent, forming a cap over the occipital pole and, again in contrast with *Tupaia*, separated from the splenium of the corpus callosum by a considerable width of cingular cortex. It may be again emphasized that the striate cortex shows an astonishing lack of differentiation.

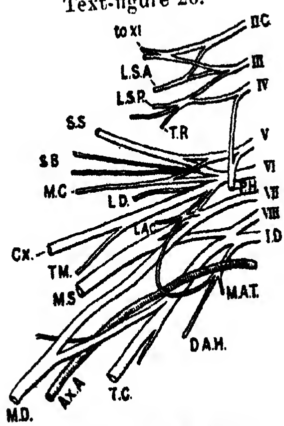
*The Spinal Cord* is about 80 mm. in length and reaches down to the back of the sacrum. There is a distinct cervical enlargement which is most evident opposite the sixth cervical vertebra. Opposite the lower lumbar vertebræ there is a faint lumbar enlargement of the cord.

Text-figure 25.




Dissection of face showing the distribution of the *N. Facialis.* (× 2.)
*Pr.O.* Præorbicularis. *Zyg.Orb.* Zygomatico-orbicularis. *Can.* Caninus. *Fac.A.* Facial artery.

Text-figure 26.



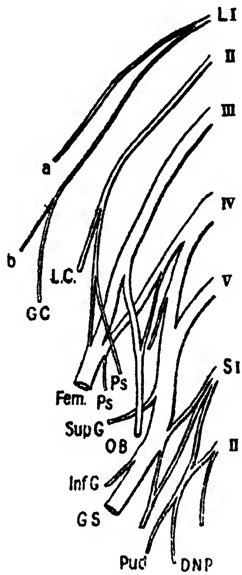

The Cervicobrachial Plexus.
*L.S.A.* Levator scap. ant. *L.S.P.* Lev. scap. post. *TR.* Trapezius. *S.S.* Suprascapular nerve. *S.B.* Subscapular n. *M.C.* Musculocutaneous. *L.D.* Latissimus dorsi. *P.H.* Phrenic. *Cx.* Circumflex n. *T.M.* Teres major. *L.A.C.* Lateral ant. thoracic. *M.S.* Musculospiral. *M.D.* Median. *Ax.A.* Axillary artery. *I.C.* Inner cord. *D.A.H.* Dorso-abdomino-humeralis. *M.A.T.* Median anterior thoracic.

## The Peripheral Nervous System.

It is unnecessary to enter into a detailed account of the peripheral nerves. The following points were recorded during the dissection of the animal and perhaps are worthy of note.

Some details of the cranial nerves are recorded in connection with the account of the special sense organs. In connection with other cranial nerves, it may be observed that the fifth nerve is large. The supraorbital nerve does not pass through a supra-orbital foramen as in *Tupaia*. The infraorbital nerve, where it issues from the antorbital foramen, is very conspicuous and breaks up into a multitude of branches supplying a rich innervation to the snout region.

Text-figure 27.




The Lumbosacral Plexus.

*a.* Iliohypogastric. *b.* Ilioinguinal. *L.C.* Lateral cutaneous. *Fem.* Femoral. *Ps.* Branches to psoas. *Sup.G.* Superior gluteal. *Ob.* Obturator. *Inf.G.* Inferior gluteal. *G.S.* Great sciatic. *Pud.* Pudic nerve. *D.N.P.* Dorsal nerve of the penis.

The *N. Facialis* emerges from the stylomastoid foramen under cover of the anterior fibres of sternomastoid and the greater part runs forwards on to the face, appearing from under the anterior border of the parotid gland. On the surface of the masseter, a rich plexus is formed, the details of which can be seen from text-fig. 25. No communicating fibres forming a plexus with the trigeminal nerve were found.

The 9th, 10th, 11th, and 12th nerves were found to have the usual distribution.

The details of the cervical and brachial plexuses can be gathered

from text-fig. 26, which is largely self-explanatory. In the arm it may be noted that the radial and external cutaneous nerves are large, the medial cutaneous nerve breaks up into three or four branches in the distal third of the upper arm which can be traced down to the middle of the medial aspect of the forearm, the external cutaneous branch of the musculocutaneous can be followed down the ventral surface of the forearm to the wrist, the lateral side of the upper arm is innervated by a conspicuous branch of the circumflex nerve, the ulnar nerve, halfway down the forearm, gives off a well-marked dorsal branch which runs beneath flexor carpi ulnaris to supply the medial side of the fifth digit and a communicating twig to the radial in the 4th cleft, and the median nerve passes through the entepicondylar foramen with a branch of the brachial artery and in the middle of the forearm gives off a well-marked palmar cutaneous twig.

The constitution of the lumbosacral plexus is indicated in text-fig. 27. In the leg it may be noted that the external cutaneous reaches the thigh by passing superficial to the inguinal ligament, and is a relatively large nerve. The peroneal nerve runs under cover of the peroneus longus muscle to reach the anterior tibial region, and its musculocutaneous branch becomes superficial by passing between peroneus longus and extensor fibularis at the middle of the leg. This nerve innervates all the interdigital clefts with the exception of the second which is supplied by the anterior tibial. The internal saphenous nerve passes anterior to the medial malleolus with the long saphenous vein.

## The Sense Organs.

### *The Visual Apparatus.*

The formation of a complete bony orbital margin has already been noted in the description of the skull. A dissection of the orbital cavity showed the usual nerves and vessels. The supra-orbital branch of the trigeminal was traced to the superior orbital margin, round which it curved on to the scalp. In *Tupaia*, this nerve passes through a supraorbital foramen. The maxillary division of the trigeminal is relatively very large. It lies in a broad groove in the floor of the orbit and passes anteriorly through the antorbital foramen on to the face. The zygomatic branch of this nerve was traced to a foramen on the orbital surface of the malar bone.

The lachrymal gland was found under cover of the dorso-lateral margin of the orbital rim. It consists of a somewhat diffuse acinous gland flattened out against the orbital surface of the frontal bone. The Harderian gland is well developed and forms a compact, lobulated, yellowish-white body about 4·5 mm. in diameter fitting tightly by a concave surface against the antero-medial surface of the eyeball. It opens on to the conjunctival sac by a number of fine ducts.

The palpebral conjunctiva and the caruncula are deeply pigmented, and the surface of the latter is covered by fine hairs. The nictitating membrane, which is also deeply pigmented, forms a triangular, rather stiff flap covering over the anterior part of the cornea. Even when this "third eyelid" is pulled to its greatest limit, however, it does not cover more than a third of the corneal surface.

The eyeball measures 6·5 mm. in diameter and the cornea, which measures 5·25 mm. in diameter, forms almost half of the globe. The optic nerve, which measures less than 1 mm. in diameter, enters the sclerotic immediately to the medial side of the posterior pole of the eye. So far as can be estimated, the optic axis lies at an angle of about 30° with the median antero-posterior plane. A dissection of the interior of the eye shows a deeply-pigmented iris and a circular pupil. The lens is large and almost spherical, its diameter measured between the margins being 4·5 mm. and between the anterior and posterior poles 4·0 mm. The fundus oculi shows a certain amount of pigmentation, especially over the periphery and on the nasal side. Elsewhere, the fundus exhibits a beautiful blue-and-silver iridescence in which the fine retinal vessels appear outlined in light blue. The optic papilla, which marks the site of entrance of the optic nerve, is a prominent raised hillock of a grayish colour. There is no depressed spot forming an optic cup. There is a complete absence of pigmentation over the papilla and over the immediately surrounding retinal area, especially to the postero-lateral side.

*Ocular Muscles.*—The usual recti and oblique muscles are present and arranged in the usual manner. The superior oblique

Text-figure 28.

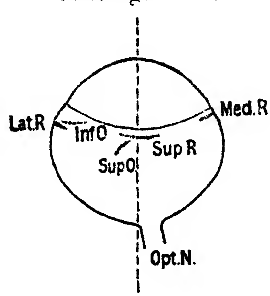



Diagram of the left eye viewed from above, indicating the points of attachment of the ocular muscles. The position of the insertion of the inferior oblique is projected through from the lower surface.

passes through a well-defined fibrous pulley and the inferior oblique rises from the orbital surface of the maxilla immediately lateral to the lachrymal bone. The levator palpebræ is present

as a fine muscular slip taking origin from the margin of the optic foramen immediately medial to the attachment of the superior rectus, and runs forward superficial to the latter muscle to reach the upper eyelid. The retractor bulbi is distinct, and forms a sheath of muscle surrounding the optic nerve and gaining insertion into the sclerotic close to the posterior pole of the eye. The attachment of the ocular muscles to the sclerotic can be seen from text-fig. 28. The muscles are all attached very close to the corneoscleral junction. The insertion of the superior oblique shows a tendency to blend with that of the superior rectus, and the tendon of the inferior oblique bears the same relation to the lateral rectus.

*The Retina.*—The preservation of the material is unfortunately not sufficiently good to enable a study to be made of the detailed histological structure of the retina. In the sections taken through the head of specimen B the retina is fragmentary, but sufficient remains to allow of some broad observations on its lamination. The pigment layer of the retina is narrow, and appears to differ little from that of *Tupaia.* The outer nuclear layer is relatively broad and crowded with nuclei, these latter being about 8–10 thick. The outer molecular layer is thin. The inner nuclear layer is about half the breadth of the outer nuclear layer, being on the average 4–6 cells in thickness. The inner molecular layer is broad, while the ganglion layer is only one cell in thickness.

Taking the whole thickness of the retina as 100, the width of the laminæ can be stated as follows :—

| | |
|---|---|
| Layer of percipient elements | 22 |
| Outer nuclear layer | 26 |
| Outer molecular layer | 10 |
| Inner nuclear layer | 15 |
| Inner molecular and ganglion layers | 37 |

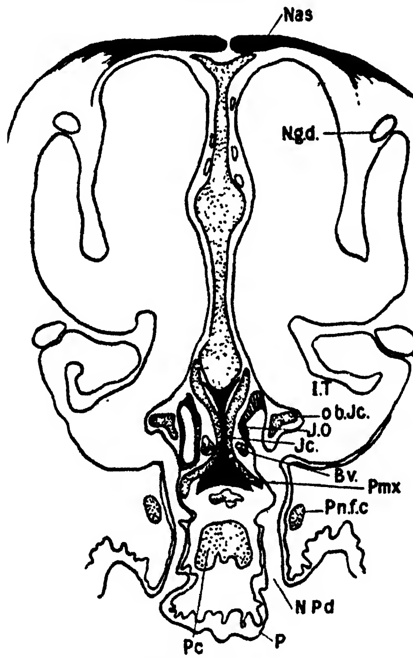
The retinal lamination contrasts very strongly with that of *Tupaia.* In the latter the outer nuclear layer is only two or three cells thick, while the inner nuclear layer is some 8–10 cells in thickness. Dr. Woollard, in a forthcoming publication, deals with the retinal lamination of mammals in some detail, and, basing our statements on his observations, it may be said that *Ptilocercus* possesses what is essentially a "rod retina," in association with nocturnal habits of life, while *Tupaia* has a retina adapted to a diurnal type of vision, in which cones predominate. Although in a given area of the retina the percipient elements may be more numerous in *Ptilocercus* than in *Tupaia*, the different type of element which predominates in the latter is certainly associated with an enhanced acuity of vision. The features of the retina, therefore, bear out the conclusions already drawn from a study of the visual centres in the brain.

The optic nerve is oval in section, measuring, on the average, 0·53 mm. by 0·40 mm. In *Tupaia* it is 0·95 mm. in diameter.

*Jacobson's Organ and the Nasal Cartilages.*

The anatomy of Jacobson's organ in *Ptilocercus* corresponds so closely to the structure in *Tupaia* that Broom's account of the organ in that animal can be applied in almost every detail here. Text-fig. 29 represents a tracing of a section passing through the nasopalatine duct, which can be seen to open directly upward

Text-figure 29.



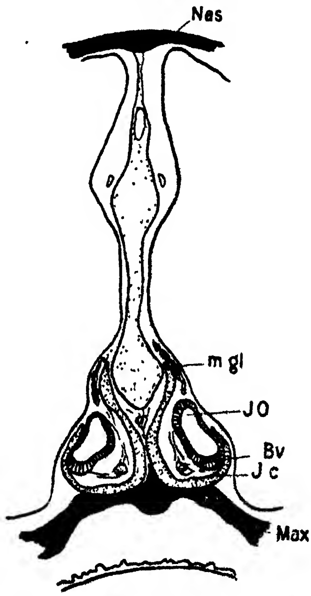

Transverse section through the nasal cavity at the level of the opening of the nasopalatine duct. Traced with a projectoscope.

*Nas.* Nasal bone. *N.g.d.* Nasal gland duct. *I.T.* Inferior turbinal. *L.d.* Lachrymal duct. *O.b.Jc.* Outer bar of Jacobson's cartilage. *J.O.* Jacobson's organ. *J.c.* Jacobson's cartilage. *B.v.* Blood-vessel. *Pmx.* Premaxilla. *P.n.f.c.* Posterior nasal floor cartilage. *N.P.d.* Nasopalatine duct. *P.* Palatine papilla. *P.c.* Papillary cartilage.

into Jacobson's organ. Jacobson's cartilages are seen to be very closely applied to each other, but separated by a thin plate of the palatine process of the premaxilla. On the lateral side of the organ can be seen the outer bar of Jacobson's cartilage. Traced forwards this becomes continuous with the dorsal part of Jacobson's cartilage, while posteriorly it joins up with the ventral part. In sections further forward Jacobson's cartilage is found to

divide into two processes, a dorsal and a ventral. The former can be followed for a considerable distance as an attenuated bar of cartilage closely applied to but not structurally continuous with the lower end of the lateral aspect of the septal cartilage, until it fades away just posterior to the point where the anterior nasal floor cartilage becomes joined up with the septal cartilage. The ventral process becomes continuous anteriorly with the recurrent nasal floor cartilage. In the most anterior sections the anterior recurrent floor cartilage connects up with the cartilage of the lateral nasal wall and forms a support for the

Text-figure 30.




Transverse section through the nasal septum immediately posterior to the opening of the nasopalatine duct, showing Jacobson's organ. Traced with a projectoscope. *Nas.* Nasal bone. *M.gl.* Mucous glands. *J.O.* Jacobson's organ. *B.v.* Blood-vessel. *J.c.* Jacobson's cartilage. *Max.* Maxilla.

maxillo-turbinal. Then it again becomes detached from the cartilage of the lateral wall, its lateral free border projecting up from the floor of the nasal cavity and having on its lateral aspect the lachrymal duct. Finally, it becomes continuous with the septal cartilage. At this level the lateral nasal wall is devoid of cartilage, except for the lower part formed from the lateral part of the alar cartilage and the dorsal part formed from the septal portion of the alar cartilage. Other points to be noted in text-fig. 29 are the relatively large size of the papilla of the palate, the large papillary cartilage which it contains, and

the small posterior nasal floor cartilage on the lateral aspect of the nasopalatine duct. Text-fig. 30 represents a tracing of a section through Jacobson's organ more posteriorly. The organ is seen to be of large size, closely pocketed in the scroll of Jacobson's cartilage, and extends back for nearly 2 mm. behind the opening of the nasopalatine duct. On its medial aspect is a single large blood-vessel, and on its lateral aspect two or three smaller vessels. Immediately dorsal to the organ is a collection of mucous glands which increases in size when traced posteriorly. Eventually Jacobson's cartilage disappears altogether, leaving a mass of mucous glands lying up against an attenuated process of cartilage which represents the posterior extremity of the septal cartilage which has been replaced dorsally by the mesethmoid. The material has not been sufficiently well preserved to allow a detailed study of the cellular structure of Jacobson's organ to be made. It is, however, lined by ciliated epithelium, and the medial wall is much thicker than the lateral. The vomer does not extend forwards far enough to come into relation with the organ as is the case in *Tupaia*.

## The Circulatory System.

### *The Cardio-vascular System.*

*The Pericardium* is a thin-walled sac enclosing the heart in the usual manner. It is very loosely attached to the diaphragm by a little diffuse connective tissue, and sterno-pericardial ligaments are represented by extremely fine bands of areolar tissue.

*The Heart* lies almost in the antero-posterior axis of the thoracic cavity. The auricles are separated anteriorly by an interval of 2 mm. or more by the commencement of the pulmonary artery. The apex of the heart is round and blunt, and both ventricles partake in its formation. The interventricular sulci are very faint grooves, and only a small portion of the left ventricle can be seen from an anterior view. The heart measures 11 mm. from base to apex and 8 mm. in breadth. The right atrial chamber shows three large openings for the two superior venæ cavæ and the inferior vena cava. The fossa ovalis is only faintly indicated, and the Eustachian valve is represented by a ridge of endocardium lying between the openings of the inferior cava and the left superior cava. The crista terminalis and the musculi pectinati are present as usual. The pulmonary veins open by a single opening into the left atrium. The valves of the heart call for no remark.

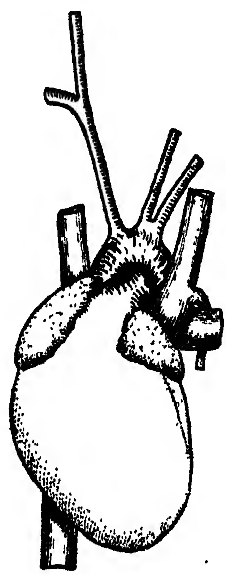
*The Aorta.*—The right innominate artery is about 6 mm. in length, and divides as usual into common carotid and subclavian branches. The left common carotid and subclavian vessels arise from the arch of the aorta by a common trunk which, however, is extremely short, varying from 0·5 mm. in Specimen A to 2·5 mm. in Specimen B. The descending aorta gives off intercostal arteries to the intercostal spaces, and enters the abdominal

cavity by passing between the crura of the diaphragm well to the left of the mid-line.

The abdominal aorta gives off the external iliac arteries at the level of the 5th lumbar vertebra, and these vessels diverge from each other at an angle of 60°. Immediately below, the aorta divides to form the internal iliac vessels. There is thus no common iliac artery.

The inferior phrenic, cœliac axis, renal, superior and inferior mesenteric, and caudal branches arise from the aorta as usual. The right renal ascends at a considerable angle in order to reach

Text-figure 31.



Heart and large vessels. (× 3.)

the hilum of the right kidney. The inferior mesenteric meets the colon wall 10 mm. below the ileo-colic junction, and divides here into ascending and descending branches. It rises from the aorta 5 mm. above the origin of the external iliacs. The lumbar arteries number three pairs. Of these, two are small and run the usual course. The middle vessel is large, and on each side runs laterally behind psoas minor and in front of psoas major. The right artery passes in front of the inferior vena cava.

The external iliac artery gives off small inferior epigastric and circumflex iliac branches.

*The Arteries of the Head and Neck.*

The common carotid runs a straight course up to the base of the skull, close to which it divides into ectocarotid and entocarotid branches. Immediately before division the common carotid gives off a small occipital branch which runs behind the bulla and is crossed by the hypoglossal nerve. The entocarotid runs into the carotid foramen on the medial side of the bulla, and its further course is described in connection with the tympanic region of the skull. The ectocarotid runs forwards deep to the stylohyoid muscle, and here divides into two main branches. Of these, one runs lateralwards over the anterior part of the bulla and supplies pre- and post-auricular vessels, a submaxillary artery, and a twig to the parotid gland. The latter supplies the superficial temporal artery, while from the submaxillary branch is derived the facial artery. The course of the facial artery can be seen from text-fig. 25. The other main terminal branch of the ectocarotid forms a lingual artery which runs forwards and medialwards and disappears among the muscles of the tongue.

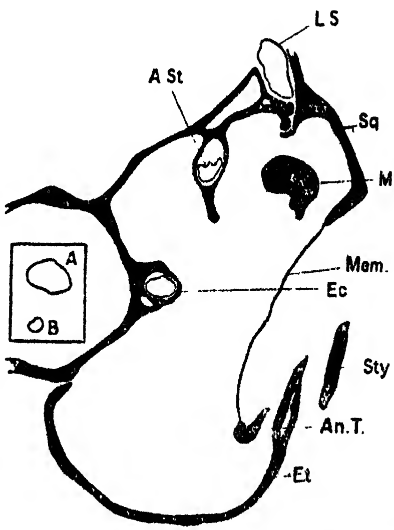
The subclavian artery in the neck gives off a conspicuous vertebral artery which can be traced up together with the vein to the transverse process of the sixth cervical vertebra through which it passes in both specimens A and B. There is also a small inferior thyroid artery and an internal mammary artery which run their usual course.

*The Course of the Entocarotid Artery through the Tympanic Cavity.*

The taxonomic importance of the course of the entocarotid artery and its branch, the stapedial artery, in the tympanic cavity has been shown to be considerable. These structures have been studied in *Ptilocercus* by means of serial sections taken through the whole head of the animal. The entocarotid pierces the bulla on its posteromedial aspect and enters an osseous canal on the medial wall of the tympanic cavity. For the rest of their course in the cavity the entocarotid and stapedial arteries remain in bony canals. After a course of a little over a millimetre the stapedial branch is given off. The latter pierces the stapes, and then runs forwards in the roof of the cavity embedded in the incomplete septum which separates the epitympanic sinus from the small loculus. It finally enters the intracranial cavity at the anterior margin of the os petrosum and close to the lateral margin of the tympanic wing of the alisphenoid. The entocarotid pursues a forward course over the convexity of the promontory, and enters the cranial cavity by passing through a notch at the posterior border of the junction of the alisphenoid and basisphenoid. So far there is complete agreement with the condition found in *Tupaia*. There are, however, certain important differences. In the first place, the entocarotid in *Ptilocercus* is much larger relatively to the

stapedial artery and also in absolute size. This can be readily seen by reference to the tracings in text-fig. 32. Here it is seen that the entocarotid and stapedial vessels are of approximately the same calibre. In *Tupaia*, on the contrary, the entocarotid, or arteria promontorii, is considerably diminished in size, its diameter being not more than one-third the diameter of the stapedial artery. Such a diminution of the arteria promontorii is a lemurine feature. Immediately before the stapedial artery enters the cranial cavity, it gives off a small branch the diameter

Text-figure 32.




Transverse section through the Tympanic Cavity. Traced with a projectoscope. Section 13·51.

*L.S.* Terminal part of the lateral venous sinus. *A.St.* Stapedial artery. *Sq.* Squamosal. *M.* Head of malleus. *Mem.* Membrana tympani. *Ec.* Entocarotid. *Sty.* Stylohyal. *An.T.* Annulus tympanicus. *E.t.* Entotympanic.

Inset are shown tracings drawn to the same scale and in a corresponding position of *A*, the stapedial artery and *B*, the entocarotid of *Tupaia*.

of which is about a third of the diameter of the continuation of the parent vessel. This branch runs ventrally in close relation to the posterior margin of the tympanic wing of the alisphenoid, and, joining the chorda tympani nerve, leaves the skull by passing through the interval between the antero-superior extremity of the annulus tympanicus and the squamosal to reach the inner part of the glenoid cavity immediately lateral to the foramen ovale. This branch is evidently the ramus inferior of the stapedial artery. I have previously demonstrated, by a study

of a complete series of serial sections through the head of *Tupaia* (lent to me by Dr. Woollard), that in this animal the ramus inferior is absent, unless it can be said to be represented by a minute twig which comes off from the stapedial artery on one side only and runs through the suture between the bulla and the alisphenoid. The importance of this feature lies in the fact that the presence of a ramus inferior is to be regarded as a primitive characteristic which is possessed by the lipotyphlous insectivores, while in Lemurs it is completely absent.

It may be noted that in *Tupaia* the stapedial artery is much more freely suspended in the bony septum in the roof of the tympanic cavity than is the case in *Ptilocercus*.

*The Arteries of the Upper Extremity.*

The subclavian artery passes over the first rib in front of and in close association with the brachial plexus. As the axillary artery, it is crossed anteriorly by the medial head of the median nerve and the communicating branch between the two anterior thoracic nerves, and gives off a large posterior circumflex branch which accompanies the circumflex nerve (N. axillaris). Continued on as the brachial artery, the vessel is crossed superficially by the median nerve which is passing to the medial side of the limb. The brachial artery gives off a well-marked superior profunda branch which accompanies the musculospiral nerve, a small inferior profunda, running with the ulnar nerve, and a medium-sized vessel which passes through the entepicondylar foramen with the median nerve. This latter branch runs with the median nerve into the forearm, and there forms the volar and dorsal interosseous vessels. The brachial artery continues superficially across the antecubital fossa and down the forearm in close association with the tendon of flexor carpi radialis. It then runs more deeply between the latter tendon and the palmaris longus to reach the median nerve just above the wrist, passing with the nerve under the transverse carpal ligament. The only branches traced were a minute twig given off below the elbow to the lateral side of the forearm and another small vessel given off at the junction of the middle and lower thirds of the forearm, which runs deep.

In the palm the main vessel breaks up into digital vessels lying superficial to the median nerve and the flexor tendons. There is apparently no formation of palmar arches.

*The Arteries of the Lower Extremity.*

The femoral artery appears from under the inguinal ligament lying on the iliopsoas muscle. About 3 mm. below its origin the femoral artery gives off two conspicuous branches, one to the medial side to the adductors and one to the lateral side representing the lateral circumflex of human anatomy. Immediately above these a small vessel arises which runs up over the

inguinal ligament to supply the large superficial lymph-node lying above the ligament. Some 7 mm. below its origin the femoral trunk gives off the saphenous artery, which is about half the size of the continuation of the femoral artery. The saphenous artery becomes superficial with its accompanying vein and nerve at the posterior border of sartorius at the junction of the middle and lower thirds of the thigh, but before doing so, it gives two muscular branches, one to gracilis and one to vastus medialis. The saphenous artery runs superficially down the medial aspect of the leg, but at its lower end it runs more deeply behind the medial malleolus, forming there the posterior tibial artery which supplies plantar branches to the sole of the foot in the usual manner.

The femoral trunk, immediately on passing through the gap in the adductor magnus, divides into two parts. One of these gives off (*a*) a muscular branch to biceps etc., and (*b*) a branch which (i.) sends a twig to semimembranosus etc., (ii.) supplies a vessel running into the gastrocnemius, and (iii.) sends an artery which joins and accompanies the lateral saphenous nerve behind the lateral malleolus and supplies digital branches to the outer toes.

The other branch of the femoral artery runs on with the tibial nerve and at the lower end of the popliteal space divides into two, one of which is continued down the posterior aspect of the leg and one which pierces the interosseous membrane to form the anterior tibial vessel. The latter accompanies the anterior tibial nerve on to the dorsum of the foot, where it supplies digital arteries to the inner toes. The sciatic artery which accompanies the sciatic nerve is small, and its distribution is muscular to the posterior region of the thigh.

*Venous System.*

The two main venous channels draining the head and neck are the external and internal jugular vessels. Of these, the former is much the larger. The external jugular vein is formed just deep to the lower border of the parotid gland by the union of (1) a submaxillary trunk which drains the submaxillary region, the tongue, and the face, and (2) the post-glenoid vein, which, after emerging from the cranial cavity through the post-glenoid foramen, runs through the substance of the parotid gland. At the clavicle the external jugular splits into two equal parts, one passing in front of and one behind the bone. These unite again under cover of the clavicle and open at once into the subclavian vein. The clavicle is thus encircled by a big venous ring. Into that part of the vein which passes superficial to the clavicle, drain tributaries from the arm (the minute cephalic vein and a superficial vein which courses over the deltoid) and from the pectoral region. The internal jugular vein is formed by a continuation of the lateral sinus in the posterior cranial fossa which leaves the skull in company with the IXth, Xth, and

XIth cranial nerves. It is joined at the base of the skull by a small tributary which is the continuation of the inferior petrosal sinus.

Of the veins of the upper extremity, it may be noted that the cephalic vein is very small and can only be traced down to the middle of the upper arm. The main superficial vein consists of a vessel which accompanies the radial nerve in the forearm and which runs up the outer side of the upper arm, over the dorsolateral aspect of the deltoid, to empty into the portion of the external jugular vein which passes in front of the clavicle.

In the lower extremity the main superficial vein is the internal saphenous, which commences in a dorsal venous arch on the dorsum of the pes, runs up in front of the medial malleolus, and joins the saphenous artery. It passes under cover of the posterior border of the sartorius with the artery and joins a tributary of the femoral vein, eventually opening into the latter at the middle of the thigh and below the origin of the saphenous artery. The inferior vena cava receives the usual tributaries. The iliac vessels conform to the arrangement of the corresponding arteries. The spermatic veins terminate as in Man.

In the thorax it is to be noted that there are two superior venæ cavæ, and that the azygos vein is situated on the left side. The former are of equal size and have the usual disposition. No cross connection between the veins of either side could be detected. Before it opens into the right auricle, the right superior vena cava receives a superior intercostal tributary which drains the upper three or four intercostal spaces of the right side. The large and conspicuous azygos vein opens into the terminal part of the left superior vena cava by arching over the root of the left lung. It runs through the diaphragm from the abdominal cavity with the aorta, and in the lower part of the thoracic cavity receives at least three tributaries, which cross over the front of the vertebral bodies and drain the lower intercostal spaces of the right side. In addition, of course, the vena azygos drains the intercostal spaces of the left side of the chest caudal to the third or fourth. It may be observed here that a similar disposition of the azygos vein has been found in all the specimens of *Tupaia* which I have examined, including a 25-mm. embryo of *Tupaia minor*.

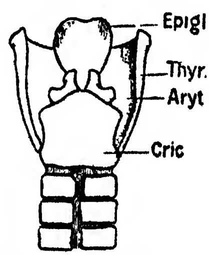
## The Respiratory System.

*The Larynx.*—The epiglottis is of the usual leaf shape. It projects up behind the palatine velum into the nasopharynx. The laminæ of the thyroid cartilage are simple quadrate plates of cartilage which show no signs of ossification. The lateral surface of each lamina shows a smooth rounded elevation corresponding to the oblique ridge found in the human structure and serving for the attachment of sternothyroid and thyrohyoid muscles. Each lamina is perforated by a small foramen which

is situated a third of the distance from the superior to the inferior borders and a third of the distance from the lateral border to the mid-line. Through this foramen passes a fine branch from the internal laryngeal nerve. There is a short blunt inferior cornu, but no superior cornu. The cricoid cartilage forms a ring which is markedly expanded in a vertical direction posteriorly. Its posterior surface is smooth. On its superior border are situated prominent arytenoid cartilages, the conspicuous feature of which is the relatively large size of the muscular processes. These cartilages appear to possess a free mobility. Viewing the larynx from inside, the false vocal cords are seen to be feebly-developed transverse folds of mucous membrane, and the laryngeal saccule represented by a mere dimple in the lateral wall of the laryngeal cavity.

The musculature of the larynx appears to be well differentiated, and the following could be readily isolated from each other—cricothyroideus, which can be divided into two bundles, a median

Text-figure 33.




Posterior view of the Larynx. (× 4.)

and a lateral; cricoarytenoideus lateralis and posticus; thyroarytenoideus; and interarytenoideus. Serial sections through the larynx confirmed the differentiation of these muscles, and showed conspicuous masses of mucous glands in the submucous tissue lining the cavity of the larynx.

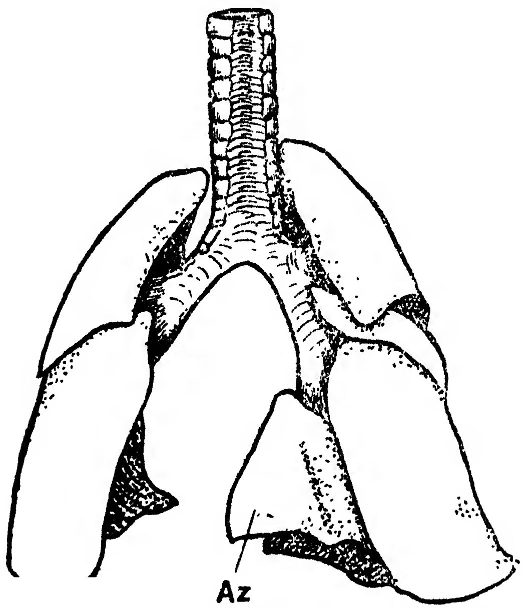
*The Trachea* measures 22 mm. in length and is composed of 21 or 22 cartilaginous rings. These are all incomplete, so that there is a well-marked gap extending down the posterior aspect of the trachea and also on to the primary and secondary bronchi. The trachea divides as usual into two bronchi. Of these, the left runs downwards and laterally for a distance of some 5 mm. and then divides into two secondary bronchi, one for each pulmonary lobe. The right bronchus quickly gives off an eparterial bronchus to the superior lobe, and later divides as on the left side. The relation between the pulmonary arteries and the bronchi is the same as that which pertains in Man.

*The Lungs* are divided into four lobes on the right side and

two lobes on the left. Of the former the inferior lobe is the largest, the middle and superior are much smaller and of equal size, while the azygos lobe is slightly smaller again. The latter bears an intimate relation to the posterior aspect of the pericardium. On the left side the superior lobe is rather less than half the size of the inferior lobe.

The fissures separating the lobes are complete. In relation

Text-figure 34.




Lungs and Trachea from behind. (× 3.) *Az.* Azygos lobe.

with the posterior aspect of the hila of the lungs are a few conspicuous lymph-glands. The pleura is disposed in the usual way.

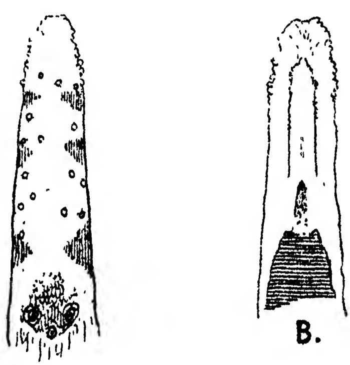
## The Digestive System.

*The Mouth.*—The palate shows a series of nine transverse ridges, all of which reach across from one side to the other. The ridges correspond one to each tooth from the second incisor backwards. Behind the first incisor and on either side of the incisive cushion which marks the position of the nasopalatine duct, is a small pit which receives the apex of the second lower incisor.

*The Tongue* is long and slender, measuring 21 mm. from the central circumvallate papilla to the tip and averaging some

5 mm. in breadth. It tapers very slightly to a rounded tip. The dorsum is richly covered by conical papillæ, on the summits of which are fine, recurved, hair-like processes. These processes are, however, too small to be detected with the naked eye. Scattered sparingly over the dorsum of the tongue, with a preference for the neighbourhood of the margin, are a few fungiform papillæ. These are small and not readily detected except on close examination. Round the margins of the tip of the tongue are many conspicuous rounded fungiform papillæ, which here form a crenated edge to the tongue. These papillæ are also very evident when the tongue is viewed from below. Posteriorly there are three circumvallate papillæ arranged in a triangle, with the apex pointing backwards. There is no lateral organ. On the under surface there is a definite sublingua.

Text-figure 35.



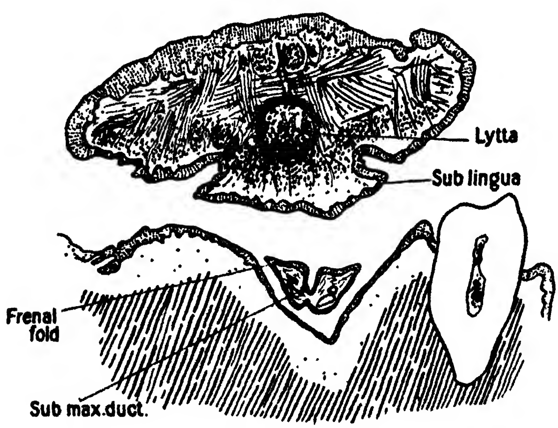

A. Dorsal aspect of Tongue. B. Ventral aspect. (× 2.)

This structure is about 2 mm. broad, and extends forward to within 2 mm. of the tip of the tongue. The tip of the sublingua is bound down to the under surface of the tongue, but the margins are free and membranous and anteriorly are irregularly serrated. The lytta of the sublingua, which in *Tupaia* forms a conspicuous median ridge, is only very faintly indicated in *Ptilocercus*. In the floor of the mouth are to be found relatively large and fleshy plicæ sublinguales or frenal folds which possess free margins and together form a free bifid tip reaching forward towards the front incisors. The margins of these folds are not serrated.

A study of serial sections through the tongue shows the following features. The lytta is well developed and extends from the level at which the tongue is attached to the floor of the mouth by the frenum as far as the tip. Its relative size may be

seen from text-fig. 36, and in the greater part of its extent it is composed of longitudinal muscle fasciculi and a central core of fat cells. It is surrounded by a thin sheath of connective tissue and circularly disposed muscle-fibres. Near the tip of the tongue, the muscle-fibres in the lytta disappear and only fatty tissue remains. The intrinsic musculature of the tongue appears to be well differentiated, and can be divided into clearly defined groups of superior and inferior longitudinal bundles along the dorsal and ventral aspects of the tongue, transverse fibres running across the centre, and vertical and oblique fibres in the lateral regions. A fine median raphe can be traced throughout the whole length of the tongue, to which the transversus linguæ fibres are attached. No mucous glands at the tip of the tongue constituting an apical gland of Nuhn are present. The sublingua

Text-figure 36.




Transverse section through the Tongue. Traced with a projectoscope.

is seen to be much more simple than it is in *Tupaia*. The fasciculi of the inferior longitudinal muscle extend into the base of the sublingua, but it has otherwise no supporting structure. The lateral margins are free. Except for a slight median elevation of the surface epithelium to be seen in some sections, there is no sign of a "keel" or lytta of the sublingua.

The free extremities of the frenal folds are shown in text-fig. 36. They here contain the ducts of the submaxillary glands which run forwards to open on to the pointed ends of the folds.

*The Salivary Glands.*—The parotid gland is large, extending over the posterior part of the masseter muscle and wrapping round the cartilaginous auditory meatus. It is pierced by the great auricular nerve, branches of the facial nerve, and the vein issuing from the post-glenoid foramen. The gland narrows down

at the lower border of the masseter to form the duct which runs along the lower border of the mandible and up along the anterior border of the masseter to pierce the buccinator and reach the buccal cavity. An isolated lobule of the parotid lies immediately below the commencement of the parotid duct in the submaxillary region. The duct from this lobule joins the main duct.

The submaxillary gland is also conspicuous and is situated behind the inferior lobule of the parotid. It is prolonged forwards above the mylohyoid muscle and its duct runs the usual course to open on the free extremity of the frenal folds.

The sublingual gland is not present as a distinct entity, but appears to be represented by the anterior lobules of the submaxillary gland.

*The Pharynx.*—The mucous membrane lining the pharynx is quite smooth. The tonsils are small yellowish oval bodies about 2 mm. in length, lying horizontally in the usual position. They are surmounted by small supratonsillar fossæ. The soft palate is some 10 mm. long, and ends posteriorly in a thickened concave border. There is no uvula. In the naso-pharynx is seen the opening of the eustachian tube above the posterior part of the soft palate and immediately behind the tip of the hamular process of the medial pterygoid plate. The opening is slit-like and is covered above by a fleshy valve-like fold of mucous membrane.

The constrictors of the pharynx are three in number and have the usual attachments. The inferior constrictor is especially conspicuous and takes a wide origin from the thyroid cartilage.

*The Œsophagus* runs a straight course to its opening in the diaphragm and exhibits no features of note. It is 42 mm. in length.

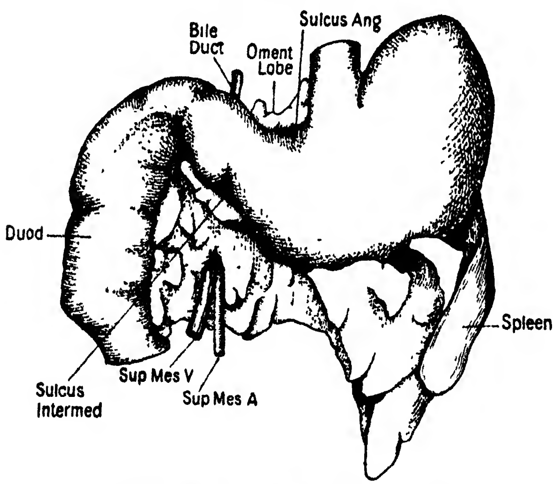
*The Peritoneum.*—The stomach has the usual peritoneal relations. The gastro-hepatic omentum stretches from the lesser curvature to the portal fissure of the liver. The great omentum is relatively short, attached above to the great curvature of the stomach, reaching to the commencement of the duodenum on the right and on to the pancreas at its left extremity. Its free border forms a rolled edge which extends across the epigastric region. The duodenum is completely surrounded by peritoneum. The spleen lies in the dorsal mesogastrium and is attached to the posterior median line by the lieno-renal ligament. The pancreas is likewise completely invested with peritoneum except where the omental lobe stretches up behind the stomach to come into relation with the lesser omentum. The dorsal mesentery of the small intestine shows a twist about the superior mesenteric artery in association with the rotation of the small gut. There is a continuous mesocolon which is attached to the posterior median line. The right surface of the mesocolon at its commencement is attached by a peritoneal fold to the mesoduodenum and directly to the posterior surface of the terminal part of the duodenum. The cæcum is invested by peritoneum except where

the mesentery runs to its right border from the terminal part of the antimesenteric border of the ileum and the adjacent part of the mesentery of the small intestine.

The Liver is attached to the diaphragm and the anterior abdominal wall by peritoneal folds which are continuous with the falciform ligament and which leave no bare area on the liver.

*The Stomach* is simple in form. It shows a well-marked fundus separated from the termination of the œsophagus by a deep notch. The incisura angularis is represented by the shallow depression at the junction of the œsophagus and the lesser curvature, while there is a faint indication of a sulcus intermedius on the great curvature indistinctly separating off the

Text-figure 37.




The Stomach, Pancreas, and Spleen. (× 3.)

pyloric canal from the rest of the viscus. An annular constriction marking the position of the pyloric sphincter is evident.

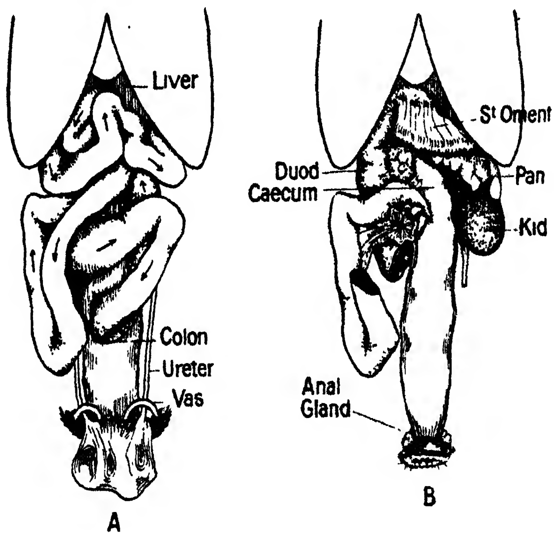
The longitudinal muscle-fibres are conspicuous on the surface. The stomach wall appears to be relatively thick with a well-marked muscular layer and a mucous membrane thrown into rugose folds. These folds tend to straighten out into parallel ridges as they approach the pylorus, but no evident differentiation of areas can be distinguished by macroscopic examination of the interior of the stomach. The appearance of the mucous membrane changes abruptly into the smooth velvety mucous membrane of the duodenum at the pyloric sphincter.

*The Small Intestine* measures about 145 mm. in length and averages 3–4 mm. in diameter. The duodenal portion passes

downwards behind the terminal part of the small intestine and becomes continuous with the jejeunum without any evident change. The coils of small intestine are arranged in no definite order. The terminal part forms a loop which descends into the right iliac region and then ascends on the right side, turning to the left at the subcostal margin to pass in front of the duodenum to meet the colon in the mid-line. There is thus a rotation of the small gut as is made evident in text-fig. 38 B.

*The Colon* is extremely primitive. It forms a straight tube which runs directly downwards from the ileo-colic junction to

Text-figure 38.

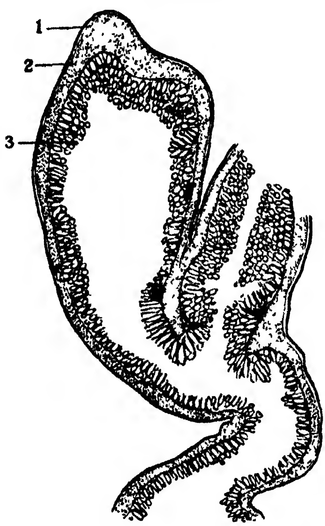



The Abdominal Cavity.
A. Small intestines in position. B. After removal of the greater part of the small intestine. (Nat. size.)

the anal canal, keeping to the mid-line. The diameter of the colon is about 7 mm., and the distance from the ileo-colic junction to the anal orfice is 29 mm. The ileo-colic opening is not marked by any valve, but is surrounded by a circular ridge of mucous membrane. There is a well-developed cæcum measuring 8 mm. in length and projecting upwards so that its tip just comes into relation with the stomach. The cæcum is conical in shape with a faint constriction at its base. In front of the ileo-colic junction are two small round lymphatic glands, and behind is a third gland of the same size. The colon forms a straight tube with no formation of sacculations.

The mucous membrane lining of the colon and rectum is generally smooth, but it becomes thrown into vertical folds some 8 mm. distance from the anal orifice. There are no transverse folds. The longitudinal muscle coat is evenly disposed around the circumference of the gut. A sharply defined ribbon-like band of this muscle becomes detached from the dorsal wall of the rectum at a point 7 mm. from the anal orifice, and runs distally to be attached by a strong tendon to the ventral aspect of the 4th caudal vertebra. This muscle, which may be termed the caudo-rectalis muscle, was found by microscopical

Text-figure 39.




Longitudinal section through the Cæcum and Ileo-cæcal junction. Traced with a projectoscope. (× 8.)

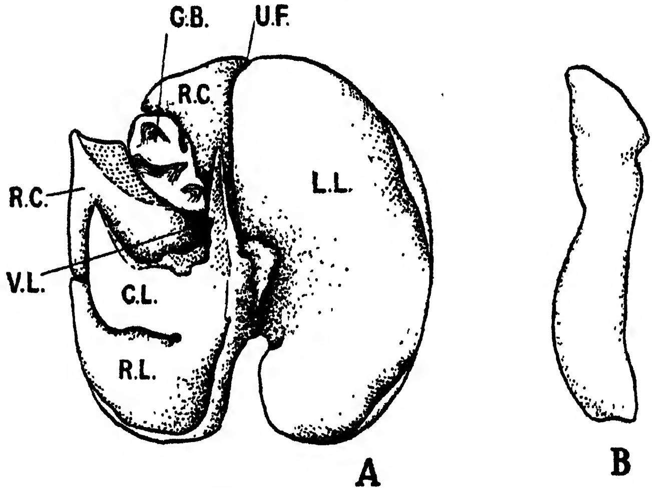
1. Serous and longitudinal muscle coat. 2. Circular muscle coat. 3. Mucous membrane.

examination to be composed mainly of unstriped fibres, though there were at least some striped fibres close to the caudal attachment.

On either side of the anal canal, above the sphincter ani externus, lies a small lobulated gland. Microscopical examination shows that the lobules are composed of numerous simple acini lined by columnar epithelium and filled with a homogeneous, colloid material. The sections also indicate that the glands open by small ducts on to the surface of the perineal region immediately lateral to the anal orifice. It may be concluded, therefore, that these are of the nature of scent glands.

*The Liver.*—This organ weighs just under 1·2 grams and measures 17 mm. in breadth by 18 mm. in antero-posterior diameter. It consists of three main lobes, the right lateral, central, and left lateral. Of these the central is the largest and the right lateral the smallest. The central lobe forms most of the diaphragmatic surface of the liver. The central lobe is subdivided into right and left central lobules by an umbilical fissure and the falciform ligament. The fissure is incomplete, being confined to the abdominal and inferior surfaces and fading away when the dorsal or diaphragmatic surface is reached.

Text-figure 40.




A. Liver, from caudal aspect. B. Spleen, viewed from right side. (× 3.)
*G.B.* Gall-bladder. *U.F.* Umbilical fissure. *R.C.* Right central lobe.
*V.L.* Venous lobe. *L.L.* Left lobe. *C.L.* Caudate lobe. *R.L.* Right lobe.

Where present, the fissure is deep. The fossa for the gall-bladder is situated in the centre of the right central lobule, and here forms a deeply excavated notch. The under surface of the left lobe is hollowed out for the reception of the stomach, and a well-marked cardiac notch indicates the position of the œsophagus. The ends of the fissure between the left lateral and the central lobes terminate immediately to the left of the upper end of the fossa for the vena cava. This fissure runs obliquely so that the left lateral lobe forms about half of the inferior aspect of the liver and less than a third of the dorsal aspect. The right lateral lobe is excavated on its lower surface where it comes into contact partly with small intestine. It has projecting down from its medial part a well-marked caudate lobe which,

however, is only about a quarter the bulk of the right lateral lobe itself. It is hollowed out by contact with the cranial half of the right kidney. Projecting down from the base of the caudate lobe are two processes which correspond to the spigelian lobe of human anatomy. One of these is the papillary process, which is small and lies in relation with the lesser curvature of the stomach. The other is a long attenuated process—the venous lobe—which projects down along and partially surrounds the inferior vena cava for a distance of 9 mm., coming into close relation below with the suprarenal glands.

*The Gall-Bladder* is relatively large. The lower half of its anterior surface comes into direct contact with the anterior abdominal wall. It is completely surrounded by peritoneum except at its neck.

The bile-ducts have the usual arrangement, the common duct passing down in the lesser omentum with the portal vein, and joining with the pancreatic duct well before it reaches the duodenal wall.

*The Pancreas* is a large gland. The pars duodenalis lies tucked in the angle between the pyloric part of the stomach and the duodenum, and is pierced by the superior mesenteric vessels. A process extends up behind the stomach to come into relation with the lesser omentum and constituting an omental lobe. The pars lienalis is extensive, lying between the lower half of the spleen and the great curvature of the stomach, and projects down in front of the left kidney where it lies up against coils of small intestine. The pancreatic duct joins the common bile-duct before the wall of the duodenum is reached, and they open by a common opening about 4 mm. from the pylorus. There is no duodenal papilla.

## The Urogenital System.

### *The Urinary Organs.*

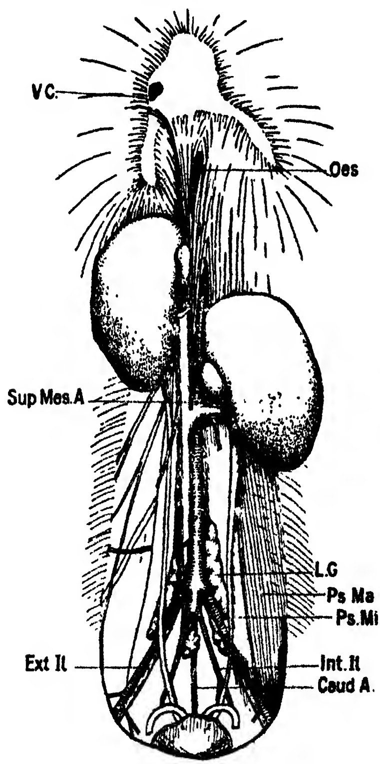
*The Kidneys* are simple in appearance, the right being situated at a considerably higher level than the left. Each measures about 12 mm. in length and 7 mm. in breadth. The upper poles are broad, but the lower poles tend to taper somewhat into blunt points. The kidneys are almost completely surrounded by peritoneum, being attached by a mesentery which runs from the hilum to the lateral aspect of the vertebral column. Section of the kidney shows that there is one large calyx which fits accurately in the pelvis and ends in a tapering point which projects into the beginning of the ureter. On the anterior wall of the pelvis of the ureter are to be found two or three small flattened plaques of medullary tissue which perhaps represent rudimentary calyces. On the posterior aspect of the hilum of each kidney is a moderate-sized lymphatic node.

*The Ureters* run a straight course down to the bladder, opening into the base of that organ by small slit-like apertures which lie

flush with the surface of the mucous membrane. The ureteric openings are close together and also close to the urethral opening.

*The Bladder* presents no features of special interest. When contracted, it has the usual pyriform shape. There is no obvious interureteric muscular ridge and the trigone is not to be readily

Text-figure 41.




Posterior Abdominal Wall. (× 2.)

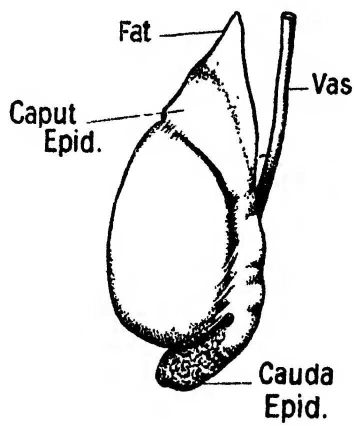
*V.C.* Caval opening. *Oes.* Œsophageal opening. *L.G.* Lymph gland. *Ps.Ma.* Psoas major. *Ps.Mi.* Psoas minor.

distinguished from the rest of the interior of the viscus except that the mucous membrane covering it is thrown into fine folds which converge below on the urethral aperture.

*The Testicle.*—The average weight of the body of the testis with the epididymis was found to be 0·08 gram. The body of

the testis is oval and slightly flattened laterally. It measures 7 mm. in its long diameter and 4 mm. dorso-ventrally. The caput epididymis is conspicuous and is surmounted by a triangular mass of subserous fat. The cauda epididymis is large and prominent, and the coils of the tube of which it is formed are very distinct. The lower end of the vas opposite the caudal third of the testis is much convoluted. Surrounding the testis is the saccus vaginalis, which is in free communication with the peritoneal cavity above. The vas and the other constituents of the spermatic cord are attached to the posterior wall of the sac by two mesenteries. The mesentery of the cord becomes continuous with the mesentery of the testis and epididymis, the latter mesentery being continued down to the lower pole of the testis. From the cord, the tunica vaginalis runs straight on to

Text-figure 42.

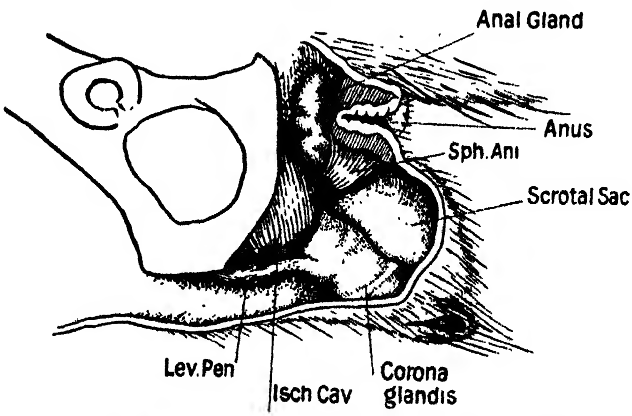



The left Testicle viewed from the lateral aspect. (× 4.)

the caput epididymis on both sides. It is further reflected from the caput and body of the epididymis directly on to the testis on the medial side, but on the lateral aspect there is formed a well-marked digital fossa. From the lower end of the vas, the tunica vaginalis is reflected off to form two crescentic folds, one running to the medial aspect of the lower pole of the testis, and one to the medial wall of the saccus vaginalis where it joins the parietal layer. The cauda epididymis is almost completely surrounded by the tunica vaginalis. In the four specimens examined the position of the testicle varied, and it appears certain that the testicle is not retained permanently in the scrotal sac as it is in *Tupaia*, for the

four specimens of *Ptilocercus* referred to were all apparently quite mature. In specimen A, the right testis was found in the scrotal cavity, and the left just within the internal abdominal ring. In specimen B, the same condition was present. In specimen C, both testes were in the abdominal cavity, each with the cauda epididymis protruding through the external abdominal ring to form a conical swelling. In specimen D, the right testicle was in the scrotum. The left scrotal sac contained only the cauda epididymis, the body of the testis being in the abdominal cavity. When the testis is in the scrotum, the cephalic pole lies at the level of the symphysis pubis and the caudal pole extends to the level of the tip of the

Text-figure 43.




Perineal Region from the side. The testicle has been removed from the scrotal sac on the left side. (× 4.)

*Sph.Ani.* Sphincter ani. *Isch.Cav.* Ischio-cavernosus. *Lev.Pen.* Levator penis.

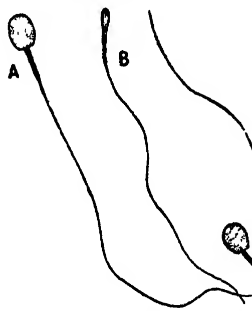
pendent penis. Relatively to the penis, therefore, as can be readily seen from text-fig 43, the scrotal sac is neither prepenial nor postpenial, but parapenial. As has been pointed out by Kaudern (19) in connection with *Tupaia*, however, the position is due rather to the direction of the body of the penis and not to any peculiarity in the position of the scrotal sac itself.

The scrotum has been described in connection with the external characters. It may be noted again that the sac is sufficiently large relative to the size of the penis to conceal the latter entirely from view except for the slit-like aperture leading into the preputial sac.

The testes are surrounded by cremaster sacs which are completely independent of each other, the strong cremaster muscle

being clearly derived from the internal oblique and the transversalis muscles. This observation appears to be confirmed by the sections taken through the cauda epididymis and the contiguous part of the abdominal wall from specimen B. These sections show that fine bundles of fibrous and unstriated muscular tissue run from the surface of the most prominent part of the cauda epididymis in among the muscle-fibres of that part of the cremaster muscle layer immediately covering it. In this region, also, the endothelial cells lining the saccus vaginalis are undergoing active proliferation and appear to be invading the cremasteric layer by the formation of numerous septa suggesting a process of excavation preparatory to the migration of the testicle into the scrotal sac. The tube of the epididymis in these sections is considerably distended with spermatozoa. The seminiferous tubules of the testis show the

Text-figure 44.




Spermatozoa, drawn from a film preparation.
A. Face view. B. Profile view.

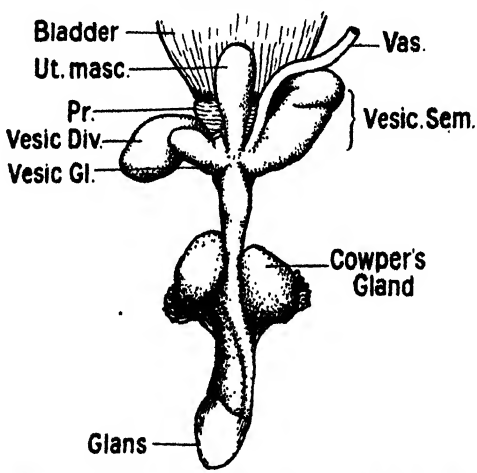
usual histological features, and the interstitial tissue was found to be scanty.

The form of the spermatozoa, as determined by staining film preparations, may be seen by reference to text-fig. 44. It will be seen that the head is flattened and ovate. The body is ill-defined. The tail is relatively long.

*The Vas Deferens*, on leaving the epididymis, runs a direct course over the lateral pelvic wall, to which it is attached by a short mesentery, until it reaches the base of the bladder. The termination of the vas bears a very intimate relation to the vesiculæ seminales, and could only be determined by a minute study of a complete series of serial sections cut throughout from the bladder to the membranous urethra. From a superficial dissection (see text-fig. 45), the vas runs down on the medial aspect of the vesicle and appears to join with the latter close to the urethra. The openings into the lumen of the urethra could

not be made out, even with a dissecting microscope. The seminal vesicles externally seem to be relatively simple lobulated bodies, divisible into two main lobules and not projecting very far above the level of the neck of the bladder. The serial sections cut through the urogenital tract of specimen B, however, showed the internal structure to be rather complicated. The seminal vesicle mass, which superficially appears fairly homogeneous, is in reality divided into two separate parts, one of which terminates below by opening separately into the urethra, and the other joining the vas immediately before the latter opens into the urethra. For purposes of distinction,

Text-figure 45.

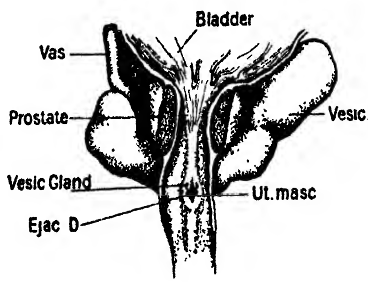



A dissection of the male Urethra viewed from the dorsal aspect
*Vesic. Sem.* Vesiculæ seminales, comprising the vesicular diverticulum of the vas, *Vesic. Div.*, and the vesicular gland, *Vesic. Gl.* (× 3.)

the former part may be called the vesicular gland and the latter the vesicular diverticulum of the vas. Both these structures are divided up internally into a complicated series of loculi, but more especially the former. The vesicular gland, moreover, is lined by proliferating masses of cubical or columnar epithelium which in many cases almost fill up the lumen of the alveoli, while the vesicular diverticulum is lined by similar epithelium more evenly arranged, leaving the alveolar cavities more open and more sacciform. The vesicular diverticulum extends up to form the upper part of the seminal vesicle (as seen on superficial dissection), and traced downwards it becomes narrowed down to form a relatively simple tube which lies

alongside and, indeed, bears a very close resemblance to, the vas itself. In this part of the diverticulum, just before it opens into the vas and also in some of the loculi in the upper part, are to be found a few spermatozoa intermingled with epithelia debris. The vesicular gland, which nowhere contains spermatozoa, apparently forms the lower lobule as seen on superficial dissection, and opens into the urethra on the margin of the orifice of the uterus masculinus immediately above and lateral to the opening of the vas. The vas deferens itself has a thick muscular wall until it reaches the level of the neck of the bladder. Here it becomes dilated somewhat, its wall is thin ed, and its simple lumen is broken up into a series of small l uli lined by epithelium very similar to that found in the vesic 'ar diverticulum. Further down, the vas narrows considerably, he loculi disappear, and the duct is joined by the duct of the vesicular diverticulum to form a very short ejaculatory duct,

Text-figure 46.




The prostatic portion of the Urethra laid open to show the openings of the ejaculatory duct, the vesicular gland, and the uterus masculinus. (× 5.)

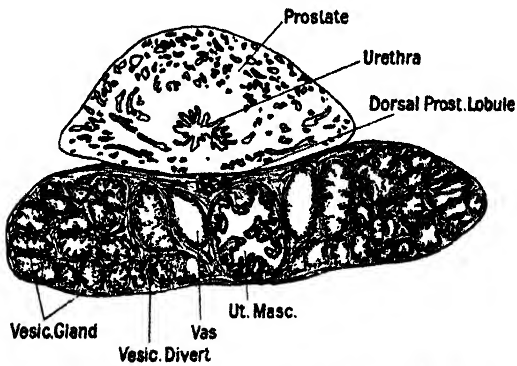
which finally opens on the margin of the orifice of the uterus masculinus immediately below and to the medial side of the opening of the vesicular gland. These two openings are extremely close together and very minute. The whole length of the vas was found to be filled with masses of spermatozoa.

*The Prostate* is a compact, ring-like gland encircling the urethra where it opens into the cavity of the bladder at the internal urinary meatus. In shape and relative size it bears a very close resemblance to the human prostate. This resemblance also applies to the appearance of a transverse section taken through the gland (see text-fig. 47) except that in *Ptilocercus* the acini are disposed all round the urethra, including the ventral aspect. The ducts are very numerous, opening into all sides of that part of the urethral canal which is enclosed by the distal half of the prostate. The stroma of the gland consists of fibrous tissue intermingled with which are strands of unstriated

muscle. A small isolated lobule of the prostate lies posteriorly, extruded from the main compact glandular mass and outside the prostatic capsule, in close association with the uterus masculinus and the seminal vesicles. The duct from this lobule opens into the floor of the prostatic urethra in company with the termination of the other prostatic ducts. This lobule is illustrated in text-fig. 47. The floor of the prostatic portion of the urethra shows a low colliculus seminalis the centre of which is pierced about 2·5 mm. from the internal urinary meatus by the opening of the uterus masculinus. A section through this part of the urethra shows the mucous membrane lining to be richly plicated.

*The Uterus Masculinus* is a simple piriform sac 5 mm. in length. It extends up the posterior aspect of the prostate and the neck of the bladder to about the same height as

Text-figure 47.




Transverse section through the prostatic Urethra.
Traced with a projectoscope. (× 15.)

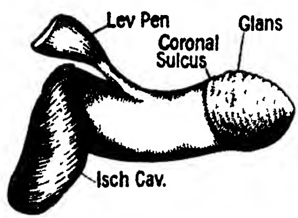
the seminal vesicles. Below, it narrows down to open into the urethra. The mucous membrane lining of this structure is covered with columnar epithelium and thrown into complicated folds. It should be noted that neither the vas, the duct of the vesicular gland, nor the uterus masculinus, passes through the substance of the prostate.

*The Membranous Urethra*, by which is here understood the urethral tract extending between the opening of the uterus masculinus and the commencement of the penile urethra, is about 5 mm. in length. The sections show that it is thin-walled and surrounded by a sphincter of striated muscle which is especially thick immediately distal to the prostate gland. As it is traced along from the prostate, the urethral wall loses its convolutions and rapidly takes on the appearance in section of a transverse slit. Alongside the distal end of the membranous

urethra lie the conspicuous bulbo-urethral glands. These are flattened, oval bodies measuring about 3·5 mm. in long diameter. Histologically, they are seen to be glands of the tubulo-acinous type, the acini being lined by columnar epithelium which is much folded and evidently in an active condition. Many of the acini are filled and even distended with a colloid material containing eosinophil granules. The lateral and superficial aspect of the gland is invested with a covering of striated muscle derived from the ischio-cavernosus, many fasciculi of which penetrate into the substance of the gland between the more superficial acini. The ducts of Cowper's glands run alongside the urethra to open a little way distal to the glands into the commencement of the penile urethra.

*The Penis* is short and stout, the penile portion of the urethra being not more than 5 mm. in length. The corpora cavernosa are strong and appear to be fairly firmly attached to the ischio-pubic arch. On surface view, the corpus spongiosum is not well

Text-figure 48.




The Penis exposed by removal of the scrotal tissues. (× 5.)
*Lev. Pen.* Levator penis muscle. *Isch.Cav.* Ischio-cavernosus muscle.

developed and certainly does not expand to form a definite bulb. At about the middle of the abdominal surface of the body of the penis is inserted the strong tendon of the levator penis muscle, while surrounding the bases of the corpora cavernosa are the prominent ischio-cavernosus muscles. The glans penis is very distinctly limited proximally by a coronal sulcus along which the mucous membrane is reflected on to the deep surface of the prepuce. This sulcus is obliquely disposed, sloping distally on to the ventral aspect where the frenum is attached. The glans penis is almond-shaped and compressed laterally. It is covered by smooth mucous membrane which in the preserved specimen is thrown into fine transverse wrinkles. There are no spines or other elevations on the surface. The glans is about 2·5 mm. in antero-posterior extent and forms distally a blunt apex. The meatal opening is a split-like aperture which extends from the tip of the glans back to the coronal sulcus on the perineal aspect. The lips of the opening are in close apposition.

The prepuce is 4 mm. in depth on its deep surface, but it is hardly distinguishable from the outside since, as already described, it is taken up into the general contour of the scrotal sac. Except, therefore, for the opening into the preputial sac, the penis is not evident on external examination.

Serial sections through the penis show the corpora cavernosa to be stout columns of cavernous tissue, enclosed in a sheath of dense fibrous tissue. The two bodies are separated by a fibrous tissue septum, the septum pectinatum, and there is no trace of an *os penis*. The corpora cavernosa are continued to the extremity of the glans penis, the two bodies being here fused together without an intervening septum. The cavernous tissue of the corpus spongiosum is feebly developed. It is more abundant on the floor of the urethral canal, and here forms a longitudinal elevation in the lumen of the urethra which gives to the latter, in transverse section, the shape of a transverse crescent the concavity of which is below. This cavernous tissue increases in amount where it surrounds the urethra in the glans. The terminal part of the urethra forms a vertical slit in section until it opens at the external urinary meatus. Except for the bulbo-urethral glands, no glands of any kind open into the penile urethra. Posteriorly, however, a small pouch-like diverticulum protrudes from the floor of the urethral canal between the lower poles of the bulbo-urethral glands. The ischio-cavernosus muscles, in these sections, are seen to be relatively large masses, but the bulbo-cavernosus is very poorly developed.

## Ductless Glands.

*The Thymus* forms a relatively large lobulated mass lying in the mediastinum and measuring 8 mm. in antero-posterior diameter and 4 mm. laterally. It extends down over the base of the heart, coming in contact with the auricles, and up in front of the trachea into the base of the neck. The two lobes are fused together, but each is prolonged cranially to form an attenuated process representing the stalk of the original diverticulum. Histologically, the usual structure of the thymus is to be seen with cortical and medullary zones and scattered Hassall's corpuscles.

*The Thyroid* consists of two lateral lobes unconnected across the mid-line by any isthmus. Each lateral lobe consists of a pale yellow elongated body about 4 mm. in length, and lying alongside the upper three or four tracheal rings. The structure of the gland as shown by histological sections calls for little remark. The vesicles are numerous, and those near the periphery of the gland are in many cases distended with colloid. In the central part of the gland, the vesicles are smaller, more closely crowded together, and there is here a considerable amount of intervesicular tissue.

*The Parathyroids* are relatively large deeply staining bodies

partially embedded in the posterior surface of the thyroid but not completely surrounded by thyroid tissue.

*The Spleen* is an elongated reddish body lying in close contact with the fundus of the stomach. It measures 16 mm. in length and has an average breadth of 3 mm. The cranial extremity is bluntly pointed while the caudal extremity is somewhat rounded. The anterior and posterior borders are slightly irregular.

*The Suprarenals* are small oval bodies of a bright yellow-ochre colour. They measure about 3 mm. in long diameter and are situated in contact with the kidneys immediately above the hila. Histologically, the gland shows the usual structure of cortex and medulla. The former is even and unconvoluted.

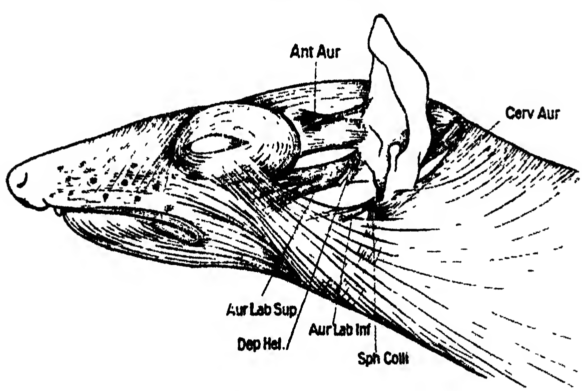
*The Pituitary Gland* was unfortunately not well enough preserved in the sections to allow a study of it to be made.

## Myology.

### *The Facial Musculature.*

In the study of these fine muscles, it was found necessary to supplement the ordinary dissecting microscope by resecting portions of the muscle-layers and examining them spread out as films under a two-thirds objective. Only was it possible, for instance, by this method to detect the muscular nature of the

Text-figure 49.




Facial Musculature. (× $\frac{4}{1}$.)

very attenuated occipitalis sheet, to demonstrate the existence of a superior auricular muscle, and to define the limits of such a muscle as the orbicularis oculi.

*The Platysma* forms a thin muscular sheet which can be traced posteriorly to a median raphe which extends from the occipital

crest where it merges with the occipitalis sheet to the upper thoracic region, over the deltoids into the upper arm, and over the proximal half of the pectoral region. From this extensive area, the fibres of the sheet converge by way of the lateral and ventral aspects of the neck towards the ocular and buccal regions. Those fibres which rise from the neighbourhood of the occipital crest curl round and gain a loose attachment to the cartilaginous concha of the ear where the latter joins the auditory meatus, forming thus a *cervico-auricularis* muscle. A fairly strong band of the platysma passes up towards the eye superficial to the auriculo-labialis superior, finally to blend with the orbicularis oculi muscle. The greater part of the muscle sheet, however, proceeds towards the angle of the mouth and passes into the upper and lower lips, freely intermingling with the fibres of the orbicularis oris and buccinator muscles. It is joined posteriorly by the auriculo-labialis inferior. The medio-ventral border of the platysma is very ill-defined, thereby contrasting with the condition found in *Tupaia* and reported in Lemurs.

The *Sphincter Colli Profundus* is present but feebly developed, consisting of a few fibres which run transversely across the ventral aspect of the neck deep to the platysma. Some of the fibres can be traced up to the cartilaginous meatus of the ear.

The *Occipitalis* muscle forms an exceedingly fine membranous sheet which extends from the occipital crest and the proximal extremity of the dorsal nuchal raphe over the roof of the skull towards the nose. The fibres blend posteriorly with those of the platysma and the auricular muscles and anteriorly with the orbicularis oculi and the muscles in the region of the upper lip. The fibres run mainly in an antero-posterior direction, but in front of the eye they diverge laterally to pass down towards the mouth. Here they form the *frontalis* component of the muscular sheet, the most anterior fibres of which run almost transversely across the dorsum of the snout from one side of the nose to the other. No bony attachment could be demonstrated in this region.

The *Orbicularis Oculi*.—This muscle consists of fibres which are disposed in the usual way, forming a very thin sheet, and blending freely at its margin with the frontalis, platysma, and auriculo-labialis superior. Attached to the anterior and posterior angles of the eye and lying altogether deep to the orbicularis oculi fibres are two very well-defined and strong muscles. The homologies of these muscles are not quite clear. The anterior muscle is firmly attached to the surface of the lachrymal bone, and possibly represents a *præorbicularis* or a *depressor tarsi* muscle. The posterior muscle gains an equally firm attachment to the anterior end of the upper border of the zygomatic arch. In my paper on the myology of *Tupaia* I called this muscle the *zygomatico-orbicularis*. It may represent a *retractor tarsi*, but this latter muscle is typically more superficial,

being merely a part of the orbicularis sheet. Both these muscles are innervated by the Facial nerve.

The *Orbicularis Oris* muscle consists of a very thin strip lying in the free borders of the lips, freely intermingling with the muscles round about, especially the platysma and the buccinator. In the upper lip is an undifferentiated mass of muscle lying deep to the nasal extension of the frontalis sheet and embedded in which are the follicles of the maxillary vibrissæ. The fibres of this muscle mass run antero-posteriorly and gain no demonstrable bony attachment. They appear to represent the mm. *Zygomatici*, *Retractor Naris*, and *Erectores Vibrissæ* which form fairly distinct muscles in *Tupaia*. Deep to this muscle, which may be here called the *musculus labium proprius*, was found a representative of the *Levator Anguli Oris* muscle, the fibres of which run downwards from the maxilla immediately distal to the infraorbital foramen to the upper lip. This muscle is very small but somewhat conspicuous because of its dark pink colour.

*The Auricular Muscles.*

The External Ear of *Ptilocercus* is well developed, and in association with this the muscles attached to it are clearly differentiated.

The posterior auricular muscle is represented by two separate slips both of which arise from the occipital crest and adjacent portion of the nuchal raphe. The anterior muscle runs forwards and laterally, and behind the ear divides into two parts. Of these, the anterior is inserted into the pinna on a little eminence which corresponds to the fossa triangularis, while the posterior is attached postero-superiorly to this. The posterior muscle runs laterally to the posterior border of the concha where the latter joins the meatus.

The superior auricular muscle is very small and difficult to identify. Its fibres are attached below to the cranial surface of the pinna and, traced upwards, they turn forwards to become continuous with the fibres of the occipitalis muscle.

The anterior group of auricular muscles is represented by a broad band which runs backwards to the cranial aspect of the base of the crus helicis, *M. Scutularis*, and a narrow slip which is attached to the dorsal aspect of the helix a little above the former, *Portio Transiens*. Both these muscles arise from the temporal fascia and blend anteriorly with the outer fibres of the orbicularis oculi. They are suppled by preauricular branches of the Facial nerve.

The *Depressor Helicis* is a small but well defined slip which runs from the anterior border of the base of the helix downwards to blend superficially with the auriculo-labialis superior.

The *Mandibulo-auricularis* is readily demonstrable as a subcylindrical muscle, somewhat darker in colour than the other muscles in the neighbourhood, passing from the deep aspect of the base of the helix to end in the fascia lying behind the

upper part of the posterior border of the masseter. No osseous attachment could be found.

The *Cervico-auricularis* has been described in connection with the platysma sheet.

*M. Auriculo-labialis Superior.*—A well defined muscle rising from the region of the tragus and passing forwards. It divides anteriorly into three slips which run deep to the upper fibres of the platysma and are lost in the tissues below the eye, blending with the fibres of the orbicularis oculi.

*M. Auriculo-labialis Inferior.*—This is represented by a small slip which is attached to the ear just in front of the incisura auris and runs forwards to intermingle with the fibres of the platysma sheet.

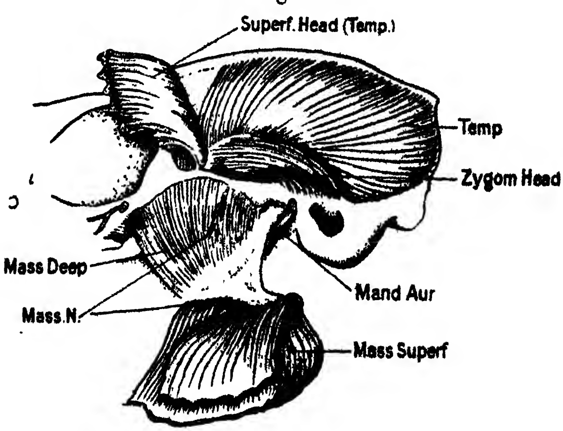
*Mm. Helicis and Tragicus* are represented by fibres running vertically between the crus helicis and the tragus, and thus forming a *M. Trago-Helicinus*. *M. Antitragicus* is also present, and is connected with the former muscle by fibres which cross over the incisura auris.

The *Mm. Obliqui* are present as longitudinal fibres stretching over the cranial surface of the pinna from the base towards the tip of the ear.

*Muscles of Mastication.*

The *Masseter* is a bulky, powerful muscle. It can with little difficulty be divided into three distinct layers. The most

Text-figure 50.




Muscles of Mastication. (×2.)

superficial layer rises from the anterior two-thirds of the lower border of the zygomatic arch. Its anterior border is markedly tendinous and is attached to the zygomatic process of the

maxilla. The fibres of this layer run almost horizontally backwards and are inserted into the angle of the mandible and the lower border for 11 mm. in front of the angle. The middle layer is separated from the superficial layer by an aponeurotic layer, but the two layers blend anteriorly. It rises from almost the whole length of the lower border of the zygomatic arch, but not extending quite so far forward in this attachment as the superficial layer. The fibres pass downwards and backwards to be inserted into the posterior part of the lower border of the mandible, but mainly into the outer surface of the angle where they form a conspicuous tendon. The deep layer consists of fleshy fibres which rise from the lower border and deep surface of the zygomatic arch and run vertically downwards to be inserted into the greater part of the lateral surface of the ascending ramus. It is pierced at the junction of its middle and posterior thirds by the masseteric branch of the trigeminal.

The *Temporal Muscle*, as in *Tupaia*, can be subdivided into three components. The superficial part takes origin from the anterior three-quarters of the temporal crest, the anterior part of the temporal fossa, and the aponeurotic surface of a corresponding extent of the deep layer. Its fibres gain an aponeurotic attachment to the anterior border of the coronoid process and ascending ramus of the mandible, reaching down to the alveolar border. The deep head rises from the remainder of the temporal crest and fossa and is inserted mainly into the anterior and posterior borders and the deep surface of the large coronoid process. The zygomatic portion rises from the upper border of the posterior end of the zygomatic arch and slightly from the deep surface, here blending with the deep layer of the masseter. It is inserted into the lateral surface of the coronoid process.

The *Digastric Muscle* is well developed. It consists of two bellies which are united by a fine oblique tendinous intersection, and not by a definite tendon as is the case in *Tupaia*. There is, however, a development of an aponeurotic surface on the lateral aspect of the junction of the two bellies. The anterior belly is aponeurotic on its lower surface at its insertion. The latter extends along the lower border of the mandible from a point 2 mm. behind the symphysis backwards for a distance of 9 mm. The two anterior bellies are united by a frail central arched tendon from which fibres arise and run directly forwards. No decussation of fibres could be detected in the mid-line. The mylohyoid nerve was observed entering its deep surface. There is no connection between the digastric and the hyoid bone. The posterior belly rises from the posterior extremity of the tympanic bulla, the occipital bone immediately behind and the adjacent margin of the stylohyal. The posterior belly is innervated from the N. Facialis.

The *Mylohyoid* muscle extends from the basihyal forwards to within 5 mm. of the symphysis. It rises as usual from the

mylohyoid ridge of the mandible, the posterior fibres passing obliquely backwards to be inserted into the whole length of the basihyal, and the anterior fibres running transversely to the median raphe. The mylohyoid nerve lies on the superficial surface of the muscle.

There is no sign of a *M. intermandibularis*.

*Pterygoideus Internus*.—This large muscle can be separated into two equal layers by an aponeurotic lamina in the centre. It rises from the whole of the pterygoid fossa and from the surface of the alisphenoid behind this as far as the level of the foramen ovale. A small tendinous slip (representing the superficial head) takes origin from the tip of the external pterygoid plate and joins the main mass. The muscle is inserted into the medial aspect of the angle of the mandible.

*Pterygoideus Externus* is small compared to the preceding muscle, but is quite conspicuous. It rises from the lateral surface of the external pterygoid plate and the adjacent surface of the alisphenoid laterally, but there is no distinct division into two heads at the origin. The insertion is mainly into the anterior aspect of the capsule of the temporomandibular joint, bony attachment being very feeble. The muscle is in contact above with the lower fibres of the deep head of the temporal muscle, but is well differentiated from this muscle.

The *Buccinator* muscle forms a thin pale layer which is attached to the posterior parts of the alveolar margins of upper and lower jaws, the fibres of which run forward into the cheek and blend intimately with those of the orbicularis oris.

The *Tensor Palati* rises from the cartilage of the auditory tube and the bulla posterolaterally. It forms a shiny aponeurotic sheet which winds round the prominent hamular process of the medial pterygoid plate to reach the palatine velum.

*Levator Palati* is a distinct muscle rising almost entirely from the cartilage of the auditory tube and slightly from the bulla medial to the tube. It passes with the tube into the nasopharynx.

### *Muscles of the Neck.*

*M. Sternomastoid*.—This muscle is broad and thick. It can be divided with little difficulty into (*a*) a sternomastoid component which is attached above by a flattened tendon to the mastoid bone immediately over the stylomastoid foramen, and below is inserted into the proximal border of the manubrium sterni; (*b*) a clavicular part which below is attached to the clavicle from the sternal extremity laterally for 7 mm. The superficial fibres of this part are attached above to the occipital crest from the mastoid to within 6 mm. of the mid-line, and the deep fibres end in the mastoid bone. The spinal accessory nerve passes between the cleido-mastoid and cleido-occipital components, and deep to the sternomastoid portion.

*M. Sternohyoid.*—Origin from the posterior surface of the manubrium sterni and insertion into the caudal border of the basihyal. The muscle is in contact with its fellow of the opposite side in the whole of its extent and gains no attachment to the clavicle.

*M. Sternothyroid.*—This muscle at its origin from the back of the manubrium sterni is closely blended with the preceding muscle. It is inserted into the lateral surface of the thyroid cartilage.

*M. Thyrohyoid* has the usual attachments to the ala of the thyroid cartilage (in continuity with the sternothyroid) and to the thyrohyal.

*M. Omohyoid* is a very slender strap of muscle attached above to the basihyal lateral to the insertion of the sternohyoid, and below to the cephalic border of the scapula close to the base of the coracoid process. Under cover of the sternomastoid, it shows a narrow oblique tendinous intersection running in a medial and caudal direction.

*M. Scalenus anticus* is absent in all the specimens examined. No muscle-fibres pass from the cervical vertebræ to the first rib superficial to the subclavian artery. Herein *Ptilocercus* contrasts with *Tupaia* in which the muscle is present.

*M. Scalenus medius.*—This muscle takes origin from the 3rd, 4th, and 5th cervical transverse processes and is inserted into the first rib immediately posterior to the subclavian artery.

*M. Scalenus posticus* is an extensive muscle which rises from the transverse processes of all except the first and last cervical vertebræ. It is inserted chiefly into the 5th rib, lateral to the rectus abdominis. At its medial margin it also gains a feeble attachment to the 2nd, 3rd, and 4th ribs, its fibres here blending partly with the lateral margin of the rectus abdominis.

*M. Rectus capitis anticus major* takes origin from the transverse processes of the 4th, 5th, 6th, and 7th cervical vertebræ and is inserted into the basioccipital as usual.

*M. Rectus capitis anticus minor.*—Origin from the lateral part of the anterior arch of the atlas and insertion into the basi-occipital bone posterior to the preceding muscle.

*M. Rectus capitis lateralis.*—This muscle is distinct, and rises from the transverse process of the atlas to be inserted into the jugular surface of the occipital bone.

*M. Splenius capitis.*—This forms a bulky muscle which rises from the whole length of the ligamentum nuchæ and the upper four dorsal spines. It is inserted into the occipital crest extending from the median line out to the mastoid bone. The lateral extremity of the insertion is aponeurotic and lies deep to and blends with the attachment here of sternomastoid. There is no *splenius colli*.

*M. Complexus* (*Semispinalis capitis*).—This muscle rises from the transverse processes of all the cervical vertebræ except the first two, and the upper two or three dorsal vertebræ. It is

inserted into the occipital bone below the occipital crest. The muscle is not divisible into separate parts and there is no sign of a *biventer cervicis*.

*M. Longissimus capitis* (*Trachelomastoid*).—This forms a well-defined strap of muscle rising from the transverse processes of the 5th and 6th cervical vertebræ and inserted into the mastoid deep to the attachment of sternomastoid.

*M. Transversalis cervicis* is an upward continuation into the neck of longissimus dorsi, and is attached to the transverse processes of all the cervical vertebræ except the first.

*M. Semispinalis colli* consists of fibres which, for the most part, rise from the transverse processes and are inserted into the spines of the cervical vertebræ. The most cranial fibres, however, do not converge on the spinous process of the axis, but pass deep to the lower border of the inferior oblique muscle to gain attachment to the transverse process of the atlas.

*M. Rectus capitis posticus superficialis.*—This is quite distinct, and forms a flattened triangular muscle rising from the spinous processes of the 2nd and 3rd cervical vertebræ, and inserted into the occipital bone immediately deep to complexus.

*M. Rectus capitis posticus major* rises from the spine of the axis and is inserted into the occipital bone deep to the complexus.

*M. Obliquus superior.*—This muscle rises from the transverse process of the atlas and is attached above as usual to the occipital bone deep to complexus.

*M. Obliquus inferior.*—This muscle is conspicuous for its bulky size. It rises from the spinous process of the axis and is inserted into the transverse process of the atlas.

*M. Rectus capitis posticus minor.*—Origin from the posterior tubercle of the atlas and insertion into the posterior margin of the foramen magnum. All these suboccipital muscles, it may be noted, are both strongly developed and well differentiated.

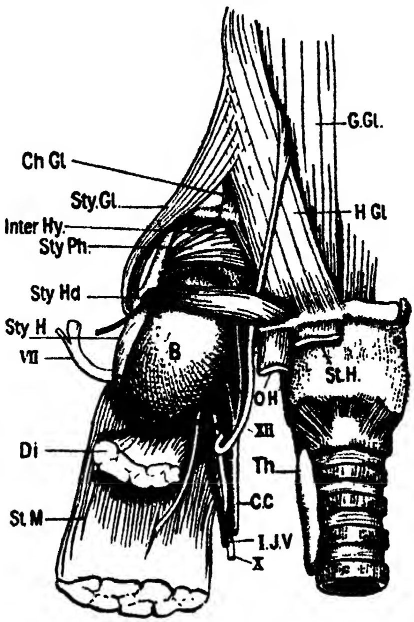
*M. Longus colli.*—This muscle may be divided into a vertical and two oblique components. The vertical portion runs between the first four dorsal vertebræ below and the last four cervical vertebræ above. The upper oblique part rises from the transverse processes of the 3rd, 4th, 5th, and 6th cervical vertebræ and is inserted partly into the front of the atlas and partly into the front of the axis. The lower oblique part rises from the bodies of the first five dorsal vertebræ and is inserted into the transverse processes of the last two cervical vertebræ.

### *The Muscles of the Tongue and Hyoid Region.*

*M. Geniohyoideus.*—This is a well-developed muscle rising from the whole of the anterior surface of the basihyal where it overlaps the hyoglossus muscle. It runs forward to end in a tendinous insertion at the lower border of the mandible extending back from the symphysis for about 2 mm. It is in close contact with its fellow of the opposite side throughout its extent. It is supplied by a twig given off by the hypoglossal trunk.

*M. Geniohyoglossus.*—This muscle is perfectly distinct from the preceding muscle. It has a small origin from the upper border of the hyoid bone and is inserted mainly into the mucous membrane of the tongue in the usual way. The lowermost fibres are attached in front to the lower border of the mandible extending back from the symphysis menti for some 4 mm. on either side.

Text-figure 51.




Stylohyoid Region. (× 4.)

*Ch.Gl.* Chondroglossus. *G.Gl.* Genioglossus. *H.Gl.* Hyoglossus. *Sty.Gl.* Styloglossus. *Inter.Hy.* Interhyoideus. *Sty.Ph.* Stylopharyngeus. *Sty.Hd.* Stylohyoideus. *Sty.H.* Stylohyal bone. *B.* Bulla. *VII.* Facial nerve. *O.H.* Omohyoid. *St.H.* Sternohyoid. *Di.* Digastricus. *XII.* Hypoglossal nerve. *Th.* Thyroid gland. *C.C.* Common Carotid artery. *St.M.* Sternomastoid. *I.J.V.* Internal jugular vein. *X.* Vagus nerve.

*M. Hyoglossus* takes origin from the thyrohyal and the basihyal, reaching to the mid-line. Running forwards the muscles diverge on either side of the genioglossus muscles to reach the lateral and dorsal aspects of the tongue. The trunk of the hypoglossal nerve enters the substance of the tongue by passing between the hyoglossus and the genioglossus muscles.

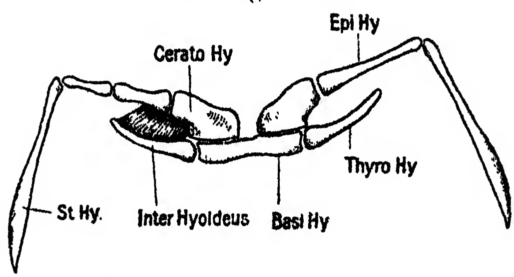
*M. Styloglossus.*—This muscle is well differentiated and rises from the lateral convex surface of the stylohyal immediately

below the external auditory meatus. It runs forwards and medially to meet the hyoglossus with which its fibres intermingle.

*M. Stylohyoideus.*—This lies altogether deep to the digastricus. It forms a rounded fleshy belly which takes origin from the lateral surface of the stylohyal. It is crossed superficially at its origin by a branch of the ectocarotid passing to the facial and submaxillary regions. Its fibres are directed medially, superficial to the hypoglossal nerve and the termination of the ectocarotid artery, to be inserted into the lateral half of the basihyal and the medial extremity of the thyrohyal. It is supplied by the facial nerve.

*M. Stylopharyngeus.*— This is a relatively thick fleshy layer of muscle which wraps over the anterior end of the rounded bulla. It rises from the anterior half of the stylohyal and its fibres run across the surface of the tympanic bulla to reach the pharyngeal wall by passing under cover of the hyoglossus and the interhyoideus. A branch was traced to the muscle from the glossopharyngeal nerve.

Text-figure 52.




The Hyoid Apparatus, showing the Interhyoideus muscle. (× 4.)

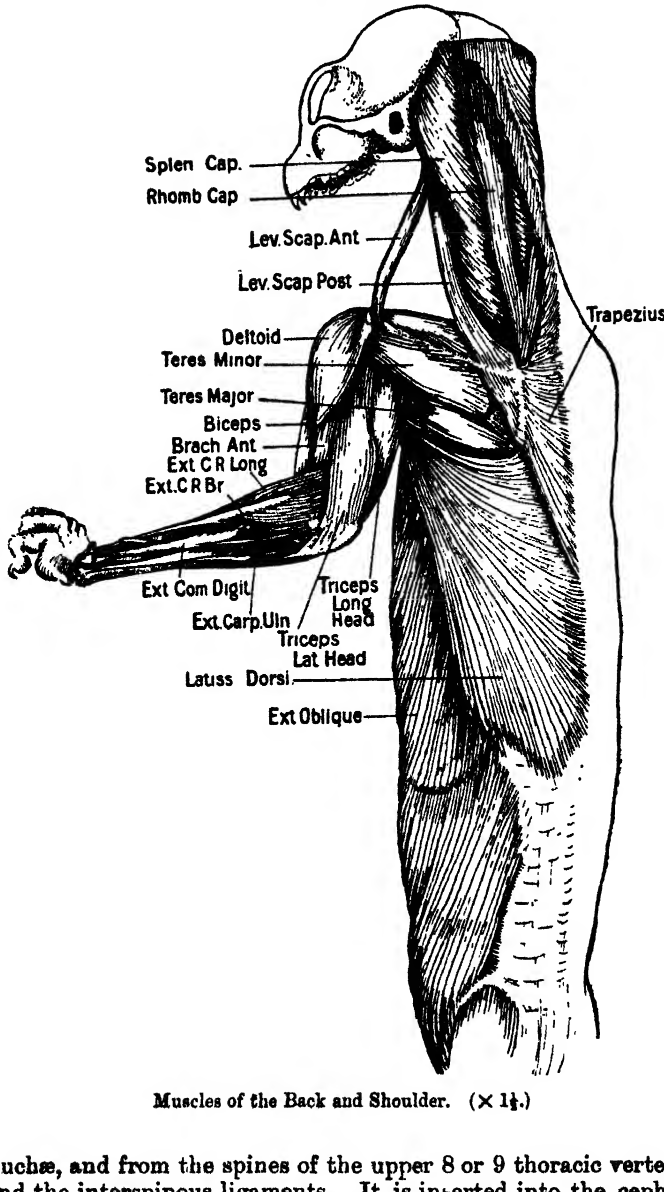
*M. Chondroglossus.*—Under this heading is described a thin but distinct layer of muscle which rises from the ceratohyal and the medial end of the epihyal and passes dorsally on the side of the genioglossus, its fibres blending with the latter muscle near the dorsum of the tongue.

*M. Interhyoideus.*—This muscle is interposed between the hyoglossus and the stylopharyngeus. It runs between the upper margin of the thyrohyal below and the ceratohyal and medial half of the epihyal above. It is innervated by the glossopharyngeal nerve. This muscle, as Dr. Edgeworth has pointed out to me, corresponds to M. subarcuatus rectus 1 of the series of longitudinal muscles found in lower vertebrates.

### *Musculature of the Dorsal and Shoulder Region.*

*M. Trapezius.*—The origin of this muscle, which forms a continuous sheet, is from the occipital protuberance, from the nuchal crest for 3 mm. from the mid-line, from the ligamentum

Text-figure 53.




Muscles of the Back and Shoulder. (× 1½.)

nuchæ, and from the spines of the upper 8 or 9 thoracic vertebræ and the interspinous ligaments. It is inserted into the cephalic lip of the free border of the scapular spine and into the medial 4 mm. of the caudal lip. There is no clavicular attachment.

*M. Latissimus dorsi* takes origin directly from the spines of the 5th to the 13th thoracic vertebræ inclusively and the interspinous ligaments, from the lumbodorsal aponeurosis, and from the lateral surface of the last three ribs. It is inserted by a characteristic flat tendon into the well-defined fossa which forms the floor of the bicipital groove on the humerus. This muscle gains no attachment to the crest of the ilium.

*M. Serratus anticus* takes origin by digitations from the upper 8 ribs. It is continuous with the levator anguli scapulæ, and is inserted into the caudal half of the vertebral border of the scapula.

*M. Rhomboideus capitis* rises from the nuchal crest deep to trapezius and sternomastoid, extending laterally from the mid-line for 4–5 mm. It takes no origin from the ligamentum nuchæ. It is inserted into the vertebral border of the scapula opposite the base of the spine, where it blends with the rhomboideus cervicis. This muscle is innervated by the same nerve which supplies the levator scapulæ posticus.

*M. Rhomboideus cervicis* is not divisible into major and minor portions. It takes origin from the upper four thoracic spines and interspinous ligaments, and is inserted into the vertebral border of the scapula caudal to the spine.

*Levator scapulæ posticus.*—This muscle, which is also known as the *Atlanto-scapularis* or the dorsal part of the *Omo-cleido-transversarius*, rises from the ventral aspect of the atlas, and is inserted into the vertebral border of the scapula just above the base of the spine and into the medial end of the upper lip of the spine.

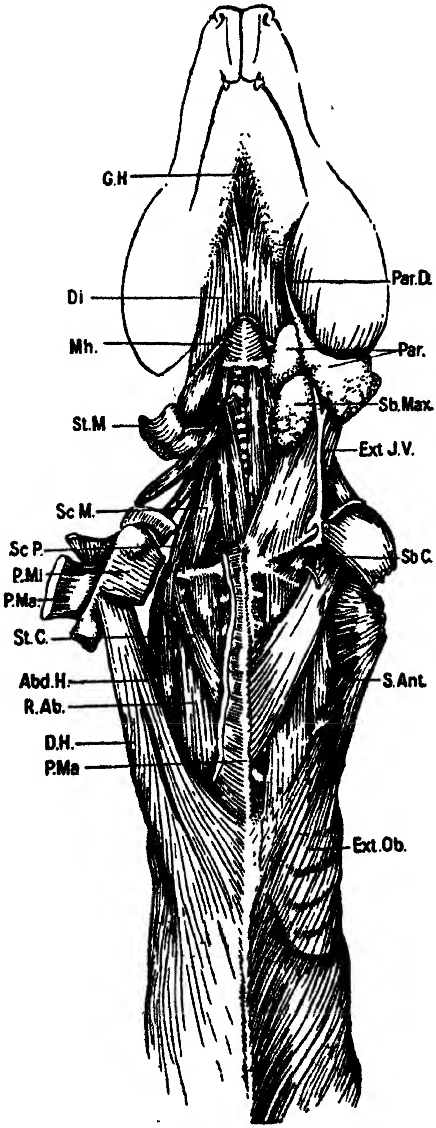
*Levator scapulæ anticus* (*Atlanto-acromialis*) rises from the atlas immediately medial to the attachment of the preceding muscle, and gains insertion into the caudal border of the metacromion process of the scapula.

*Levator anguli scapulæ.*—This muscle takes origin by a series of digitations from the transverse processes of all the cervical vertebræ except the first, immediately posterior to the scalenus posticus. It is inserted into the vertebral border of the scapula proximal to the base of the spine and continuous directly with the attachment of the serratus anticus.

### *Muscles of the Upper Extremity.*

*M. Pectoralis Major.*—This muscle cannot be divided into separate parts. It takes a continuous origin from the lower end of the tendon of the sternomastoid, from the medial extremity of the clavicle (very slight attachment), from the capsule of the sterno-clavicular joint, from the whole length of the sternum, the xiphisternum, the sternal ends of the costal cartilages, and slightly from the upper end of the rectus sheath. It is inserted in the usual fasion into the outer lip of the bicipital groove, extending from the distal end of the deltoid eminence upwards for 6 mm. This muscle is supplied by the lateral anterior

Text-figure 54.




Musculature of the Trunk. (x 1½.)

*G.H.* Geniohyoid. *Di.* Digastric. *Mh.* Mylohyoid. *Par.* Parotid gland. *Par.D.* Parotid duct. *Sb.Max.* Submaxillary gland. *Sc.M.* Scalenus medius. *Sc.P.* Scalenus posticus. *Sb.C.* Subclavius. *P.Ma.* Pectoralis major. *P.Mi.* Pectoralis minor. *St.C.* Sternocostalis. *Abd.H.* Abdomino-humeralis. *D.H.* Dorso-humeralis. *R.Ab.* Rectus abdominalis. *S.Ant.* Serratus anticus.

thoracic nerve which enters the deep surface of the muscle by passing deep to the subclavius, and by the medial anterior thoracic which pierces pectoralis minor.

*M. Pectoralis Minor* is incompletely separated from the pectoralis major at the lower part of its origin. It rises from the 4th to 7th costal cartilages and adjacent part of the sternum, and is pierced by the medial anterior thoracic nerve which supplies it. The muscle is inserted by a thin tendinous expansion into the capsule of the shoulder-joint, the great tuberosity, the lateral border of the bicipital groove, and the fascia covering the tendon of the long head of biceps, extending down the shaft of the humerus for 8 mm.

*Mm. Abdomino- and Dorso-humeralis.*—These muscles arise by a common tendon which is attached to the neck of the humerus deep to the insertion of pectoralis minor, extending down the humeral shaft for 5 mm. The two muscles become separated at a distance of about 8 mm. from their origin. The abdomino-humeralis runs towards the mid-ventral line, spreading out over the rectus sheath. Its proximal border is contiguous and blends with the caudal borders of pectoralis major and minor. The dorso-humeralis spreads over the flank, forming an extensive panniculus which reaches from the lower abdominal region over the outer side of the thigh to the base of the tail. Both these muscles are innervated by a nerve which is derived from the medial cord of the brachial plexus in common with the medial anterior thoracic nerve, and which runs to its destination under cover of the pectoralis minor muscle.

*M. Subclavius.*—This is a relatively bulky muscle which takes origin from the first costal cartilage close to the sternum, and is inserted into the lower and posterior aspects of the lateral extremity of the clavicle. There is no attachment to the scapula.

The *Deltoid* consists of two parts at its origin. The clavicular head rises from the lateral 6 mm. of the anterior border of the clavicle, and the acromial head takes origin by a well-defined tendon from the metacromial tubercle. The insertion is into the prominent deltoid crest on the humerus, where it blends with the lower fibres of the pectoralis major.

*Teres major.*—This rises from the inferior angle and the whole length of the axillary border of the scapula, and is inserted as usual into the medial margin of the bicipital groove.

*Teres minor.*—This muscle is relatively large. It rises from the lateral three-quarters of the scapular spine and the fascia covering the lateral part of infraspinatus to a corresponding extent. It is inserted into the shaft of the humerus by a flat tendon 3 mm. broad. This tendon lies deep to the deltoid, its lower fibres blending with the insertion of the deltoid. A branch of the axillary nerve was traced into the teres minor.

*M. Subscapularis.*—This rises from the whole of the ventral surface of the scapula. It is pierced by three subscapular nerves

which divide the muscle indistinctly into four parts. Each of these parts shows a somewhat bipenniform arrangement of its fibres and becomes tendinous towards the insertion into the lesser tuberosity of the humerus.

*Mm. Supra- and Infraspinatus.*—Both these muscles are powerfully developed. The former rises from the supraspinous fossa and the proximal surface of the spine, the latter from the hollowed-out infraspinous fossa and the distal surface of the spine. They are inserted into the greater tuberosity of the humerus.

*Triceps.*—This muscle is somewhat complicated. It consists of (*a*) a long head, which takes origin from the infraglenoid ridge of the scapula, forms a thick belly, and is inserted into the tip of the olecranon process superficially; (*b*) a lateral head which can be subdivided into a portion which rises by a tendinous attachment from the postero-internal aspect of the neck of the humerus, above the insertion of teres minor and lateral to the proximal extremity of brachialis anticus, and also from the fascia covering brachialis anticus; a portion rising by a linear fleshy origin from the posterior surface of the humerus medial to brachialis anticus extending from the neck down the shaft for 6 mm.; a third portion which blends closely with the preceding portion but lies on a deeper plane and rises also from the back of the humerus lateral to the musculospiral groove and is partly tendinous below. The first and second parts of the lateral head are inserted in common into the lateral border of the olecranon process and into the deep fascia covering the extensor muscles of the forearm. The third part is associated at its insertion with the long head, gaining attachment to the tip of the olecranon process. (*c*) The medial head of the triceps is small, rising from the humeral shaft extending from the middle of the inner aspect down over the lower half of the posterior surface. It is inserted deeply into the common tendon of insertion.

*M. Anconeus* is not present as a separate muscle. It is represented by the lower fibres of the medial head of triceps rising from the back of the spinator ridge and being inserted into the radial margin of the olecranon process.

*Biceps.*—The long head rises from the upper margin of the glenoid cavity and forms a relatively thick tendon which runs through the cavity of the shoulder-joint. The short head is well formed and rises from the apex of the coracoid process in common with the coracobrachialis, the tendon of the latter muscle also giving attachment to some of the fibres. The two heads join about 5 mm. below the tip of the coracoid process. The tendon of insertion is strongly attached to the radial tubercle. No lacertus fibrosus is present.

*M. Coraco-brachialis.*—This muscle is in its generalised form. The short head is fleshy, rises from the lower surface and medial margin of the coracoid process, and is inserted into the medial lip of the bicipital groove proximal to the insertion of latissimus

dorsi. The long head is tendinous at its origin from the tip of the coracoid process, and is inserted into the medial border of the humerus extending from the middle of the shaft down across the entepicondylar foramen to the medial epicondyle of the humerus. The musculocutaneous nerve passes between these two portions and supplies them.

*M. Brachialis Anticus.*—Origin from the anterior surface of the lower half of the humerus and extending upwards postero-lateral to the deltoid to reach the posterior aspect of the neck of the humerus. The muscle is inserted as usual into the coronoid process of the ulna.

*M. Dorso-epitrochlearis.*—As in *Tupaia*, this muscle rises by two heads, but they are not so distinctly separable. It takes origin mainly from the tendon of latissimus dorsi, a few fibres only coming from the adjacent tendon of teres major. The lower attachment is to the medial side of the olecranon process.

*M. Condylo-Olecranonis.*—This forms a muscular layer crossing over the ulnar nerve from the lower end of the medial supra-condylar ridge to the olecranon process, blending below with the upper fibres of the extensor carpi ulnaris.

*Muscles of the Forearm.*

*M. Brachioradialis.*—This is found to be completely absent, and in this feature *Ptilocercus* resembles the Lipotyphla and stands in contrast to *Tupaia*, in which this muscle is normally present (at least in sp. *minor* and *ferruginea*).

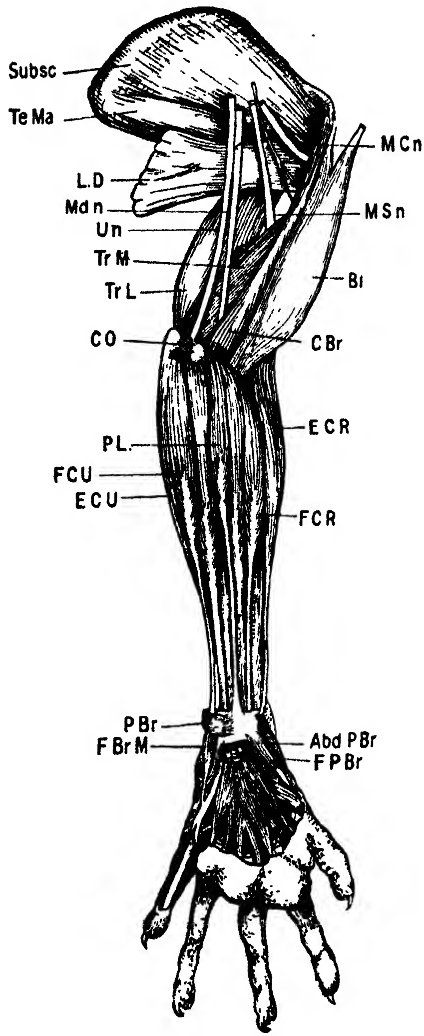
*M. Supinator* rises by a rounded tendon from the lateral epicondyle, the lateral aspect of the capsule of the elbow-joint and the small sesamoid bone situated here. There is no ulnar attachment. Inserted by fleshy fibres into the anterior and lateral aspects of the upper half of the radius. The posterior interosseous nerve passes altogether deep to the muscle.

*Mm. Extensores Carpi Radialis and Brevis* rise by a continuous origin from the supinator ridge of the humerus, extending up from the lateral epicondyle for some 5 mm. Tendons are formed at a distance of 14 mm. from the origin, and the insertions are, as usual, into the bases of the 2nd and 3rd metacarpals.

*Extensor Communis Digitorum* rises from the lateral epicondyle and intermuscular septa. Tendons are formed at the middle of the forearm and are ultimately inserted into the terminal phalanges of the ulnar four digits, aponeurotic expansions being formed on the dorsal aspect of the proximal phalanges which are intimately blended with the capsules of the interphalangeal joints. The division of the tendons of this muscle is liable to variation, but in one specimen two tendons were first formed, of which the radial supplied the 2nd and 3rd digits, and the ulnar the 3rd, 4th, and 5th digits.

*Extensor Digitorum Lateralis.*—This muscle rises in common with the former, but quickly becomes separated. It forms a long

Text-figure 55.




Muscles of the Forelimb. (× 2.)

*L.D.* Latissimus dorsi. *M.C.n.* Musculocutaneous nerve. *Md.n.* Median nerve. *U.n.* Ulnar nerve. *M.S.n.* Musculospiral nerve. *Tr.M.* Medial head of triceps. *Tr.L.* Long head of triceps. *Bi.* Biceps. *C.Br.* Coracobrachialis. *C.O.* Condylo-olecranon. *P.L.* Palmaris longus. *E.C.R.* Extensor carpi radialis longus. *F.C.U.* Flexor carpi ulnaris. *E.C.U.* Extensor carpi ulnaris. *F.C.R.* Flexor carpi radialis. *P.Br.* Palmaris brevis. *F.Br.M.* Flexor brevis manus. *Abd.P.Br.* Abductor pollicis brevis. *F.P.Br.* Flexor pollicis brevis.

tendon which below the wrist divides into two to pass to the 4th and 5th digits, fusing with the corresponding tendons of the extensor communis.

*Extensor Carpi Ulnaris.*—Origin from the lateral epicondyle and intermuscular septa. No attachment to ulna. Insertion into the base of the 5th metacarpal.

*M. Abductor Pollicis Longus.*—This is a large muscle rising from the proximal half of the posterior surfaces of the radius and ulna, extending up on to the lateral surface of the olecranon, and from a corresponding extent of the interosseous membrane. It is inserted by a stout tendon into the base of the 1st metacarpal.

*Extensor Pollicis Longus.*—This muscle can be readily separated from the remainder of the deep extensor mass up to its origin from the lateral surface of the base of the olecranon. The tendon is inserted into the terminal phalanx of the pollex.

There is no *Extensor Pollicis Brevis.*

*Extensor Profundus Digitorum.*—This muscle rises from the lateral aspect of the ulna, extending from the base of the olecranon down the upper third of the shaft. It supplies tendons to the index and medius digits, joining the corresponding tendons of the extensor communis. This and the preceding muscle lie at their origin between the Extensor Carpi Ulnaris and the shaft of the ulna.

*M. Pronator Radii Teres.*—There is no ulnar head. The muscle is well developed, and takes origin from the medial epicondyle. It is inserted by a broad tendinous attachment to the middle of the lateral aspect of the shaft of the radius.

*Flexor Carpi Radialis* rises by the common flexor tendon from the medial epicondyle of the humerus. It becomes tendinous just below the middle of the arm and is inserted into the base of the 2nd metacarpal.

*Palmaris Longus* has a similar origin to the preceding muscle. It becomes tendinous a little above the middle of the forearm, and at the proximal border of the transverse carpal ligament it spreads out to become continuous with the palmar fascia and with the transverse carpal ligament itself. The palmar aponeurosis is relatively poorly developed.

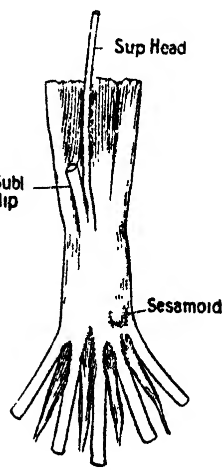
*Flexor Carpi Ulnaris.*—This arises from the medial epicondyle of the humerus and the upper half of the posterior border of the ulna. At the wrist its tendon splits into two parts, a larger portion which is inserted into the pisiform bone and a smaller slip which runs to the 5th metacarpal bone, immediately distal to the base.

*Flexor Sublimis Digitorum.*—There is no radial head to this muscle, the origin being entirely from the medial epicondyle in association with the common flexor mass. The muscle forms four tendons some 3 or 4 mm. above the level of the wrist which pass beneath the transverse carpal ligament to the four ulnar digits. Opposite the metacarpo-phalangeal joints each tendon splits to allow the passage of the deep flexor tendon, and finally

gains insertion into the middle phalanx. The tendon to the minimus digit is joined immediately before it splits by the fine tendon of the flexor brevis manus. Above the wrist a strong tendon is given off from the deep aspect of the flexor sublimis to join the flexor profundus digitorum.

*Flexor Profundus Digitorum* is a large muscle rising from several sources. A small superficial head takes origin from the deep aspect of the common flexor tendon from the medial epicondyle and ends in a fine tendon. The main mass rises from the front of the radius from the bicipital tubercle down to the proximal border of pronator quadratus, from anterior and medial surfaces of the ulna up to the base of the olecranon process, and from a corresponding extent of the interosseous membrane. At

Text-figure 56.




Palmar tendons of Flexor Profundus Digitorum.

the wrist this mass becomes indistinctly divided into three parts, lateral, central, and medial, which fuse together again to form a broad flattened common tendon. This receives on its superficial surface the communication from the flexor sublimis and the tendon of the superficial head, and in the palm divides into five tendons which pass to reach terminal phalanges of the five digits. In the common palmar tendon is developed a small sesamoid bone at the base of the tendon for the pollex. The superficial part is supplied direct from the median nerve, and the deep part by the volar interosseous and ulnar nerves.

*The Pronator Quadratus* is well developed. It extends between the radius and ulna for a distance of 5½ mm. from the lower extremity upwards.

No *M. Radio-Ulnaris* apart from the pronator quadratus was detected.

*Muscles of the Hand.*

The *Palmaris Brevis* is very distinct. Its fibres run transversely from the palmar aspect of the transverse carpal ligament and the palmar fascia to the integument on the ulnar side of the hypothenar eminence.

*Mm. Lumbricales.*—These are four in number and very conspicuous. They rise from the origins of the separate tendons of the flexor profundus, each muscle rising from the two tendons between which it lies. They pass round the radial side of their respective digits to reach the dorsal extensor expansions, but mainly to be attached to the proximal phalanges.

*M. Abductor Pollicis Brevis* is a thin attenuated muscle which rises from the transverse carpal ligament and slightly from the ossicle on the Os Trapezoideum. It terminates in a fine tendon which is inserted into the radial side of the base of the proximal phalanx and the radial sesamoid bone of the thumb.

*M. Flexor Brevis Pollicis.*—This is a bulky muscle which rises from the transverse carpal ligament, the ossicle on the palmar aspect of the Os Trapezoideum, and the adjacent part of the carpus, and is inserted into the base of the proximal phalanx, the distal extremity of the first metacarpal, and the capsule of the metacarpo-phalangeal joint mainly on the radial side, though some fibres pass also to the medial side. No separate *Opponens Pollicis* is present.

*Flexor Brevis Manus.*—This very delicate muscle rises from the ulnar region of the transverse carpal ligament, and supplies a fine tendon which joins the tendon of flexor sublimis to the 5th digit before it splits. In *Tupaia*, it may here be noted, the flexor brevis manus replaces the minimus tendon of flexor sublimis altogether.

*M. Abductor Minimi Digiti* is a broad muscle which rises from the pisiform bone and the adjacent part of the carpal ligament and is inserted into the ulnar side of the base of the proximal phalanx of the 5th digit.

*M. Flexor Brevis Minimi Digiti.*—Also well developed, rising from the transverse carpal ligament and having the same insertion as the abductor. No *Opponens* is present.

*Mm. Contrahentes.*—These muscles are three in number. They rise from the palmar surface of the carpus deep to the long flexor tendons and are very distinct. One is inserted into the ulnar side of the base of the proximal phalanx of the thumb, forming an *Adductor Pollicis*, and the others bear the same relation to the ulnar side of the index and the radial side of the minimus digits.

*Mm. Flexores Breves Digitorum.*—These are numerous, a more or less differentiated pair being found in connection with each digit. Each pair rises by a common fleshy mass from the palmar aspect of the carpus deep to the Mm. Contrahentes, lies on the palmar aspect of the metacarpal bone, and divides into its two component parts, which wrap round the distal half of this

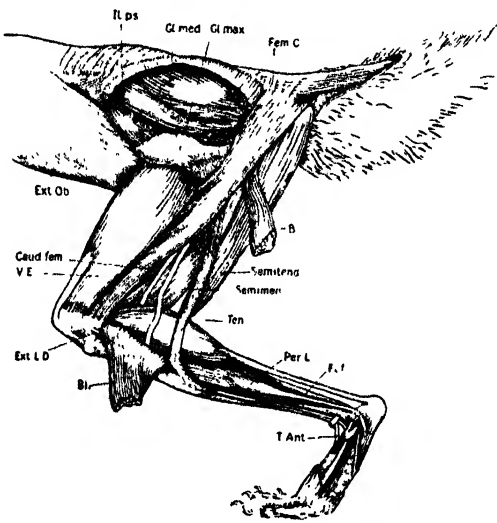
bone to be inserted into the sides of the proximal phalanges through the sesamoid bones.

*Mm. Interossei*, apart from the flexor brevis digitorum muscles just described, are not present.

*The Musculature of the Lower Extremity.*

*Gluteus Maximus.*—This muscle covers over the greater part of the gluteal region, forming a thin lamina except at the caudal border, which is thick and rounded. It rises from the crest of

Text-figure 57.




Musculature of the lateral aspect of the Thigh and Leg. (× ⅘.)

*Il.ps.* Iliopsoas. *Gl.med.* Gluteus medius. *Gl.max.* Gluteus maximus. *Fem.C.* Femoro-coccygeus. *Ext.Ob.* External oblique. *Caud.fem.* Caudofemoralis. *V.E.* Vastus externus. *Bi.* Biceps. *Semitend.* Semitendinosus. *Semimem.* Semimembranosus. *Ten.* Tenuissimus. *Ext.L.D.* Extensor longus digitorum. *Per.L.* Peroneus longus. *Fl.f.* Flexor fibularis. *T.Ant.* Tibialis anticus.

the ilium, extending back from the anterior superior spine to the dorsal border, and from the lumbodorsal fascia, through which it gains an indirect attachment to the spines of the sacral vertebræ. The most anterior fibres are inserted into the fascia lata of the thigh, and presumably represent a *tensor fasciæ femoris*. This muscle is therefore undifferentiated in *Ptilocercus*, corresponding to the condition which also obtains (according to my own studies) in *Tupaia*. The remainder of the gluteus maximus is inserted, as usual, into the third trochanter of the femur.

*M. Femoro-coccygeus* is fused with the gluteus maximus at its origin, but is otherwise distinct. It takes origin from the spines of the first two caudal vertebræ through the fascia covering the dorsal aspect of the base of the tail, and from the transverse processes of the first three caudal vertebræ. It is inserted into the femur by a series of fleshy slips extending from immediately below the third trochanter down to the lateral aspect of the lateral condyle, to the capsule of the knee-joint at the side of the patella and patellar ligament, and to the lateral fabella and the tendon of origin of the lateral head of gastrocnemius. Two branches of the sciatic nerve (distinct from the gluteal nerves) were traced into this muscle, one entering it near its origin and one at the middle of its length.

The *Gluteus Medius* is of considerable bulk and partially bilaminar. It rises from the greater part of the lateral surface of the dorsum ilii and to a slight extent from the fascia covering the caudal muscles. The superficial fibres end in a fleshy attachment to the femur from the base of the great trochanter down to the insertion of gluteus maximus. The deep portion has a tendinous insertion into the lateral aspect of the great trochanter.

*Gluteus Minimus.*—This muscle can readily be distinguished from the preceding muscle. It rises from the dorsum ilii along the ventral border, extending from the anterior superior spine back to the neighbourhood of the acetabulum. It is inserted by a tendon into the anterior surface of the great trochanter.

*M. Piriformis.*—This is represented by a thin attenuated layer of muscle which rises from the sharp dorsal border of the ilium corresponding to the great sacro-sciatic notch. The cranial fibres at their origin are continuous with the caudal fibres of gluteus medius, but the muscle at its insertion converges on the tip of the great trochanter, where it is inserted separately deep to gluteus medius. It is, moreover, supplied by a separate twig arising independently from the sacral plexus.

*M. Obturator Internus* rises from the pelvic aspect of the obturator membrane and the whole circumference of the obturator foramen. It forms a strong tendon which runs in the usual way to be inserted into the medial aspect of the tip of the great trochanter.

The *Gemellus superior* and *Gemellus inferior* are both present but indistinctly separated from each other. They arise as usual from the margins of the lesser sacro-sciatic notch and pass with the tendon of the obturator internus (which they cover over and conceal) to the same insertion.

*M. Quadratus femoris.*—This muscle rises from the lateral aspect of the tuber ischii, and is inserted into the femur from the tip of the great trochanter down to the posterior surface of the lesser trochanter. It is a well-developed fleshy muscle.

*M. Caudofemoralis.*—This conspicuous muscle takes origin from the transverse processes of the first and second caudal vertebræ,

its origin being continuous caudally with that of semitendinosus. It passes down medial to the great sciatic nerve and lateral to the branch of this nerve which runs to the semimembranosus and biceps, eventually to be inserted into the greater part of the posterior surface of the lower half of the femoral shaft, reaching down to the articular condyles. The nerve-supply is derived from the great sciatic nerve by the same twig which innervates the biceps and semimembranosus.

*M. Tenuissimus* is present as a narrow band of muscle rising from the fascia lying between the origin of the caudal fibres of gluteus maximus and the dorsal caudal muscle. It is inserted into the fascia of the leg below and in continuity with the insertion of biceps, being overlapped slightly by the lower margin of the latter muscle. It receives a twig from the nerve going to the femoro-coccygeus.

*M. Biceps* rises by a tendinous origin from the ischial tuberosity in common with the ischial head of semitendinosus. It forms a thick muscle which emerges from under cover of the posterior border of femoro-coccygeus, and is inserted by a broad fascial expansion into the lateral condyle of the tibia and the deep fascia of the leg for the upper half of its extent. It gains no attachment to the fibula.

*M. Semitendinosus*, as in *Tupaia*, has two heads of origin: (*a*) from the transverse processes of the 2nd and 3rd caudal vertebræ, blending with the origin of caudofemoralis and deep to femoro-coccygeus; and (*b*) from the ischial tuberosity in common with the biceps. Both origins are by fleshy fibres, and they unite about 6 mm. from their attachments to form a single muscle belly. This is inserted by a narrow, flat, ribbon-like tendon into the tubercle of the tibia deep to the gracilis. No tendinous intersection is visible in this muscle.

*M. Semimembranosus.*—This muscle rises from the ischial tuberosity and along the lower border of the ischium in front for 2 mm. It is inserted into the inner condyle of the tibia by a flattened tendon which passes beneath the internal lateral ligament of the knee-joint and lies deep to the upper fibres of the sartorius at its attachment to the tibia. There is no femoral attachment.

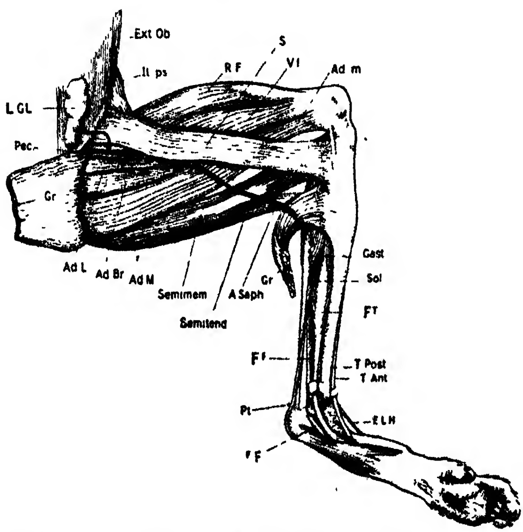
*M. Sartorius* rises from the central portion of the inguinal ligament, having no direct attachment to the ilium or the pubis. It is inserted into the mesial surface of the tibia, extending from the medial condyle downwards for some 5 mm.

*M. Gracilis* is a broad sheet of muscle, its breadth at its origin being 9 mm. It rises from the medial end of the superior ramus of the pubis, the medial end of the inguinal ligament, and the bone at the side of the symphysis pubis. It is inserted into the tibial crest for a distance of 6 mm. below sartorius by a thin aponeurosis, being slightly overlapped by the lower border of sartorius above.

*M. Pectineus.*—This is a relatively bulky muscle, rising from the body of the pubis and the medial end of the superior ramus. It is inserted into the posterior aspect of the femur extending from the lesser trochanter to the junction of the upper and middle thirds of the shaft. It is supplied by a branch from the anterior crural nerve.

*M. Adductor longus* is a somewhat narrow muscle, rising by a small rounded tendon from the side of the anterior end of

Text-figure 58.




Musculature of medial aspect of the Thigh and Leg. (× ⅓.)

*Ext.Ob.* External oblique. *L.Gl.* Lymphatic gland. *Il.ps.* Iliopsoas. *Pec.* Pectineus. *Gr.* Gracilis. *Ad.L.* Adductor longus. *Ad.Br.* Adductor brevis. *Ad.M.* Adductor magnus. *R.F.* Rectus femoris. *S.* Sartorius. *V.I.* Vastus internus. *A.Saph.* Saphenous artery. *Gast.* Gastrocnemius. *Sol.* Soleus. *F.T.* Flexor tibialis. *F.F.* Flexor fibularis. *T.Post.* Tibialis posticus. *T.Ant.* Tibialis anticus. *Pl.* Plantaris. *E.L.H.* Extensor longus hallucis.

the symphysis pubis, lateral to the origin of adductor brevis, and inserted into the middle of the femoral shaft for 3 or 4 mm. in continuity with the insertion of pectineus.

*M. Adductor brevis*, in contrast to the preceding muscle, is thick and well developed. It rises from the pubis lateral to the anterior part of the symphysis pubis and is inserted into the middle third of the femoral shaft.

*M. Adductor magnus.*—This large muscle rises from the ischio-pubic ramus, extending from immediately in front of the

attachment of semimembranosus to the symphysis pubis. It has no attachment to the tuber ischii. The bulk of the muscle runs straight down towards the knee, where it gains attachment to the posterior aspect of the medial condyle of the femur, the medial fabella, the upper end of the internal lateral ligament, the medial part of the popliteal surface, and the posterior aspect of the shaft of the femur, extending up for about 6 mm. It blends at its insertion with the caudofemoralis. The upper part of the adductor magnus, which is much smaller and is easily separated from the part already described up to its origin, forms a thin lamina which is inserted into the posteromesial aspect of the femur from the level of the upper end of the third trochanter down to about the middle of the shaft. That all this muscle-mass represents the adductor magnus is indicated by the relation which it bears to the obturator nerve, which lies entirely in front of it. Two twigs from the obturator nerve were traced to the muscle, one to each part. There is no innervation from the sciatic nerve. The femoral vessels pass through the relatively wide gap between the two parts.

*M. Obturator externus.*—This is a very well-developed muscle which takes the usual origin from the obturator membrane and the bony margin of the foramen, extending from just in front of the ischial tuberosity on to the body of the pubis, and ends in a stout tendon lying deep to quadratus femoris and being inserted into the digital fossa of the femur. It is pierced by the obturator nerve, no part of which issues from the obturator foramen by passing entirely in front of the muscle.

*M. Rectus femoris.*—This rises from the anterior inferior spine of the ilium and by a stronger tendinous attachment to the cephalic border of the acetabulum, but these two "heads" are closely blended with each other. The deep surface of the muscle is aponeurotic and the insertion is into the upper border of the patella.

*M. Vastus lateralis* is a bulky muscle which rises entirely from the anterior aspect of the great trochanter immediately below the insertion of gluteus minimus. It is inserted into the lateral side of the common quadriceps tendon, and by a fascial expansion into the lateral margin of the patella.

*M. Vastus medialis* is likewise well developed, and takes origin from the upper three-quarters of the postero-mesial aspect of the shaft of the femur, extending up in front of the lesser trochanter to reach the anterior aspect of the base of the great trochanter where it lies deep to the origin of vastus lateralis. Inserted into the medial side of the common quadriceps tendon and into the medial patellar margin.

*M. Vastus intermedius.*—This muscle is perfectly differentiated and rises from the lower two-thirds of the anterior surface of the femoral shaft by fleshy fibres. Inserted into the upper margin of the patella. No separate *subcrureus* muscle could be distinguished.

In close association with the insertion of *femoro-coccygeus* are some deeply-situated muscle-fibres running from the lateral femoral condyle to the lateral margin of the patella.

*M. Tibialis anticus* is a large muscle, rising from the upper two-thirds of the lateral surface of the tibia, the upper quarter of the antero-mesial aspect of the fibula, and the interosseous membrane. Its tendon is inserted into the base of the first metatarsal, having no direct attachment to the internal cuneiform bone.

*M. Extensor longus digitorum.*—As in *Tupaia*, this muscle rises entirely from the lateral condyle of the femur by a rounded tendon which is attached immediately in front of the upper attachment of the external lateral ligament of the knee-joint. Half-way down the leg the tendon of the muscle is formed. Just above the ankle-joint this passes through a pulley attached to the lateral aspect of the base of the lateral malleolus, together with the tendons of tibialis anticus and extensor longus hallucis. Immediately below the ankle-joint the tendon passes through a pulley of its own, which is attached by two slips, one to the front of the tip of the lateral malleolus and one to the dorsal surface of the os calcis. On the dorsum of the foot the tendon splits into four to supply the lateral four digits, fusing with the corresponding tendons of the extensor brevis and peronei to gain attachment to the middle and terminal phalanges.

*M. Extensor hallucis* is a slender muscle blending at its origin with tibialis anticus. It rises from the second quarter of the antero-mesial aspect of the fibula and from the middle two quarters of the interosseous membrane. A slender tendon is formed at the junction of the middle and lower thirds of the leg which passes under a pulley with tibialis anticus as described above, and is finally inserted into the base of the terminal phalanx of the hallux.

*M. Peroneus longus* rises from the upper half of the antero-lateral surface of the fibula, reaching on to the head of the bone, from the lateral condyle of the tibia by a small tendinous slip, and from the inter-muscular septum between it and the anterior tibial compartment. The tendon of the muscle passes over a groove on the lateral aspect of the prominent peroneal tubercle on the os calcis and across the sole of the foot in the usual way, to gain insertion into the base of the first metatarsal. There is no sesamoid body developed in the tendon.

*M. Peroneus brevis.*—This muscle is relatively large, and rises from the upper three-quarters of the antero-lateral aspect of the fibula, reaching up to the base of the head. Its tendon runs with the tendons of the two succeeding muscles above the peroneal tubercle, where they are bound down by a strap of fascia to the dorsal aspect of the os calcis. It is inserted into the base of the 5th metatarsal.

*M. Peroneus quinti digiti.*—This slender muscle takes origin

from the lower half of the first quarter of the lateral aspect of the fibula, and the fascia over peroneus brevis and between it and flexor fibularis. Its fine tendon passes behind the lateral malleolus and runs to the fifth digit, where it fuses with the corresponding tendon of extensor longus digitorum.

*M. Peroneus quarti digiti.*—This muscle is quite distinct from the preceding muscle, and rises from the second quarter of the lateral aspect of the fibula, lateral to the origin of the peroneus brevis. It ends in a fine tendon which eventually reaches the fourth digit, blending with the corresponding tendon of the extensor longus digitorum.

*M. Extensor brevis digitorum.*—This muscle rises entirely from the dorsal aspect of the os calcis and the fascia overlying it, having no attachment to the fibula. The inner part of the muscle which supplies a tendon for the hallux is definitely separated from the remainder of the muscle to form an *extensor brevis hallucis*. The tendon to the hallux joins with that of the long extensor to be inserted into the distal phalanx. The extensor brevis digitorum provides two other tendons which bear a similar relation to the 2nd and 3rd digits.

*M. Popliteus.*—This rises by a rounded tendon from the lateral condyle of the femur immediately below the origin of extensor longus digitorum, and is inserted into slightly more than the upper quarter of the posterior surface of the tibial shaft.

*M. Gastrocnemius* rises by two heads as usual, one from the lateral condyle of the femur, postero-inferior to the insertion of femoro-coccygeus, and one from the medial condyle immediately posterior to the insertion of the adductor magnus. Fabellæ are developed in both heads. The muscle becomes tendinous just above the middle of the leg and is inserted into the tuberosity of the os calcis.

*M. Plantaris.*—This very slender muscle rises mainly from the fascial sheath covering the lateral head of gastrocnemius. It ends in a fine tendon 13 mm. in length, which curls round the medial side of the tendo Achillis to reach its superficial aspect and to become continuous with the plantar fascia.

*M. Soleus* is a weak muscle, rising only from the posterior aspect of the head of the fibula and becoming tendinous some 10 mm. above the heel. It forms a minor portion of the tendo Achillis.

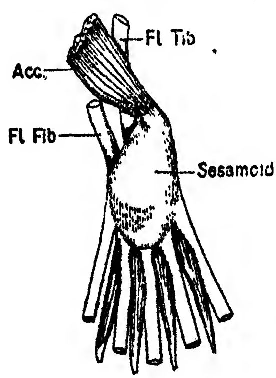
*Flexor tibialis.*—This is a large muscle, rising from the posterior surface of the upper half of the shaft of the tibia and the back of the head above the popliteus, from the fascia over tibialis posticus and over flexor fibularis, by an aponeurotic slip from the posterior aspect of the head of the fibula immediately below the origin of soleus, and from the fascia over popliteus.

*Flexor fibularis* is also a well-developed muscle, rising from the lower two-fifths of the posterior surface of the tibia,

the whole length of the posterior surface of the fibula, the middle two quarters of the interosseous membrane, and the septum separating it from the peronei muscles. The muscle remains fleshy down to the level of the ankle-joint. The insertion of this and the preceding muscle will be considered in connection with the muscles of the sole of the foot.

*M. Tibialis posticus.*—This muscle is a slender muscle which takes origin from the medial aspect of the upper third of the fibula, reaching up to the head of the bone and the fascia between it and flexor fibularis. At its origin it lies superficial to the latter muscle. The belly is about 10 mm. long only, ending in a long tendon which is much smaller than that of flexor tibialis. The tendons of these two muscles pass through a fibrous pulley attached to a tubercle projecting from the

Text-figure 59.




The long flexor tendons of the sole of the Foot and the Plantar Sesamoid. (×3.)

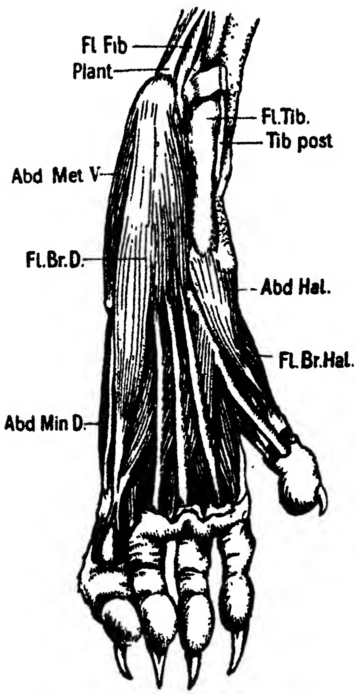
medial side of the tibia 3 mm. above the tip of the medial malleolus. Tibialis posticus is inserted on the plantar aspect of the scaphoid bone of the tarsus.

No *Rotator fibulæ* or anything corresponding to a tibio-fibularis was detected.

*M. Flexor brevis digitorum.*—This muscle is well developed and shows a generalised condition. It supplies four tendons to the four outer digits, and each of these tendons has two heads of origin, one from the lower surface of the sesamoid bone developed in the long flexor tendons and the proximal ends of the flexor tendons emerging from the anterior margin of the sesamoid, and one from the tuberosity of the os calcis either by direct muscular attachment or indirectly through the plantar fascia. While the large superficial head supplying the 5th digit is derived mainly from the deep aspect of the

plantar fascia, the superficial heads supplying the other three digits are derived from fleshy fibres which gain direct attachment to the os calcis, the three tendons being formed on the dorsal surface of this muscle-mass. This muscle is therefore similar to that of *Tupaia*, but is better developed in that each tendon has two well-formed heads of origin. The common tendons behave in the usual way, splitting over the proximal

Text-figure 60.




The musculature of the Sole of the Foot. (× 3.)

*Fl.Fib.* Flexor fibularis. *Plant.* Plantaris. *Fl.Tib.* Flexor tibialis. *Tib.post.* Tibialis posticus. *Abd.Met.5.* Abductor metacarpi digiti quinti. *Fl.Br.D.* Flexor brevis digitorum *Abd.Hal.* Abductor hallucis. *Fl.Br.Hal.* Flexor brevis hallucis. *Abd.Min.D.* Abductor minimi digiti.

phalanges to allow the deep flexor tendons to pass through, and gaining insertion into the middle phalanges.

It may be noted here that the plantar fascia is thin and inconspicuous except for a thickened strand by which it is attached to the base of the fifth metatarsal.

*M. Abductor hallucis* is a thin pale muscle, rising from the plantar fascia, the ossicle on the infero-mesial aspect of the

internal cuneiform, and by a few fibres from the sheath of the deep flexor tendons. It is inserted into the medial side of the base of the proximal phalanx of the hallux.

*M. Abductor minimi digiti* is well developed and rises from the inferior aspect and lateral margin of the tuberosity of the os calcis. It ends in a strong tendon which is inserted into the lateral side of the base of the proximal phalanx of the little toe.

*M. Abductor ossis metatarsi quinti.*—This is also a bulky muscle, taking origin from the tuberosity and the lateral surface of the posterior part of the os calcis. Inserted into the lateral side of the base of the fifth metatarsal bone.

*M. Flexor brevis hallucis* rises by two heads, the medial from the base of the first metatarsal, the internal cuneiform, and by a tendinous slip from the under surface of the anterior part of the os calcis, and the lateral from the base of the first metatarsal only. Each head is inserted into its own side of the base of the proximal phalanx.

*M. Flexor brevis minimi digiti* is a large muscle which rises from the sheath of the peroneus longus tendon by a strong attachment and from the greater part of the length of the lower surface of the 5th metatarsal. It is inserted into both sides of the proximal phalanx of the 5th digit.

*The deep flexor tendons.*—Immediately after passing into the sole of the foot the tendon of the flexor tibialis shows a well-marked thickening. This tendon, with that of flexor fibularis, ends in a bony plaque, formed as an ossification in the fused flexor tendon mass. This plaque is oval in shape, about 4 mm. long by 2 mm. broad. The long flexor tendons are inserted into the upper aspect of the posterior part of the lateral margin, the tendon of the flexor tibialis lying posterior at its attachment. From the anterior convex margin of the ossicle spring the five tendons for the toes. It is thus not possible to determine from which long flexor muscle each flexor tendon to the toes is derived. This plantar sesamoid is identical with that found in *Tupaia* by myself (6) and in the Dasypodidæ by Windle and Parsons (25). Similar sesamoids are reported in *Notoryctes* by Thompson and Hillier (30) and in *Cænolestes* by Osgood (24).

*M. Accessorius.*—This is well developed and rises by a tendinous origin from the peroneal tubercle on the lateral aspect of the os calcis. It is inserted by a tendon into the postero-medial angle of the plantar sesamoid, passing below the long flexor tendons to reach this.

*M. Contrahentes.*—These are three in number. The first rises from the bases of the 2nd and 3rd metatarsals and the sheath of peroneus longus tendon, and is inserted into the lateral side of the base of the proximal phalanx of the hallux. The other two rise from a tendinous raphe between them which extends distally almost to the level of the metatarso-phalangeal

joints, from the fascia covering the subjacent flexor breves digitorum muscles, and, to a slight extent, from the sheath of peroneus longus. The medial of these two is inserted into the lateral side of the proximal phalanx of the 2nd digit, and the lateral into the medial side of the base of the proximal phalanx of the 5th digit.

*M. Lumbricales.*—These are four in number and rise in the usual way from the deep flexor tendons. Each rises from two tendons with the exception of the fourth, which is attached to the lateral side of the tendon to the 4th digit only. The lumbricals wind round the medial side of their respective digits to reach the dorsal expansions of the extensor tendons.

*M. Flexor breves profundi.*—Including those of the 1st and 5th digits already described, each toe possesses a pair of short flexors. Each pair rises from the base of the corresponding metatarsal, from a raphe which extends along the plantar aspect of the metatarsal, and from the intermusclar septa between the muscles, and is inserted into either side of the base of the proximal phalanx. Apart from these short flexors, there are no interossei.

*Vertebral Musculature.*

*M. Serratus posticus.*—This muscle-sheet could not be distinctly separated into superior and inferior portions. It is inserted into all the ribs with the exception of the first, its fibres all running laterally and slightly caudally to be attached to the lateral surface of the ribs about 9 mm. from the mid-line. Owing to the breadth of the ribs, the serrations are not well defined.

*M. Iliocostalis.*—This element of the erector spinæ mass is not well differentiated from the adjacent muscles. Its takes origin from the crest and posterior part of the medial surface of the ilium, and forms a bulky muscle which is inserted into the angles of the lower 4 or 5 ribs. It is succeeded above by a series of muscle-strips corresponding to the *accessorius* and *cervicalis ascendens* of human anatomy, which are attached to the angles of all the ribs and the transverse processes of the lower cervical vertebræ.

*M. Longissimus dorsi* emerges from the main mass of the sacrolumbalis, through which it gains attachment to the iliac crest, the sacrum, and the lower lumbar vertebræ. Its superficial fibres are inserted into the ribs laterally, and the spinous processes of the lumbar and lower thoracic vertebræ medially. Its deep fibres are attached by strong tendons to the transverse processes of the thoracic vertebræ. On the medial side of this muscle are some strong vertical tendons which rise from the metapophyses of the last three or four thoracic vertebræ and run up to the level of the 4th, 5th, and 6th vertebræ. They give off fleshy fibres in a bipenniform manner which are attached laterally to the transverse processes and medially to the spines of the vertebræ. The medial fibres are continued upwards as a well-developed

semispinalis colli. Below the 13th vertebra, situated in the same relative position, are to be found a series of strong tendons which are attached above to the lower border of the laminæ (immediately lateral to the mid-line) of the last two thoracic and the upper lumbar vertebræ. These tendons also give off fibres in a bipenniform manner which are directed caudally and are inserted into the spines and transverse processes of the lumbar and sacral vertebræ.

*The Multifidus*, represented by short fleshy fibres passing from transverse processes to spines, is found in the lower region of the spine and is not very prominently developed.

*Semispinalis dorsi* is represented by a continuous series of short fusiform muscles passing between the transverse processes and spines of adjacent vertebræ. No long intersegmental fasciculi of this muscle are present.

*Spinalis dorsi*, consisting of fibres passing between spines over more than one vertebra, is absent.

*Levatores costarum.*—These small muscles are well developed. They rise from the tranverse processes of the thoracic vertebræ, where they blend with the medial deep attachments of longissimus dorsi, and are inserted into the broad outer surfaces of the ribs close to the costo-transverse articulations.

*Interspinales* are present throughout the length of the vertebral column down to the sacrum.

### *Perineal and Caudal Musculature.*

*Pubococcygeus.*—This forms a thin fleshy triangular muscle which takes origin from the posterior surface of the body and the cephalic ramus of the pubis, extending back to the iliopubic junction. Its origin is 7 mm. in length, and it is here separated from the iliococcygeus by a conspicuous gap through which passes the obturator nerve. The muscle is inserted at the mid-line into the aponeurosis covering the ventral caudal muscles opposite the 1st and 2nd caudal vertebræ.

*Iliococcygeus* takes origin from the medial aspect of the ilium close to the anterior margin and extends up almost to the sacroiliac articulation. It forms three well-developed tendons which are inserted into the chevron bones corresponding to the 2nd, 3rd, and 4th caudal vertebræ, intermingling with the tendons of the sacrococcygeus.

*Ischiococcygeus* lies in a more dorsal plane. It is quite well developed, consisting of short muscular fibres which rise from the medial aspect of the ischium and are inserted into the transverse processes of the last sacral and the first two caudal vertebræ.

*The External Sphincter Ani* is a thick muscle which gains a strong attachment anteriorly to the ventral aspect of the bulb of the penis.

*The Ischiocavernosus* is likewise powerfully developed, forming

a hemispherical mass of muscle rising from the distal border of the middle part of the ischiopubic ramus and wrapping round the corpus cavernosum, to the surface of which it is strongly attached.

*Bulbocavernosus.*—This muscle is very feebly developed, consisting of a few fibres which appear to be prolonged from the external anal sphincter on to the perineal surface of the bulb of the penis.

*Levator penis.*—This is a well-defined fusiform muscle attached above to the lower border of the symphysis pubis and below by a tendinous insertion to the abdominal surface of the penis in the mid-line.

*Sacrococcygeus* forms a bulky muscle imperfectly divided into a lateral and medial part, the latter constituting the infracoccygeus muscle. It rises from the transverse processes and the lateral side of the ventral aspect of the bodies of the last lumbar, all the sacral, and the first three or four caudal vertebræ. It terminates in a series of long slender tendons which run along the ventral aspect of the tail and gain insertion into the ventral aspect of the caudal vertebræ and chevron bones.

*Abductor caudæ externus*, which is indistinctly separable from the following muscle, takes origin very largely from the lumbodorsal fascia, and also to a slight extent from the dorsal part of the iliac crest. It runs down to the transverse processes of the caudal vertebræ.

*Extensor caudæ lateralis* is a downward continuation of the longissimus dorsi muscle. It rises from the transverse processes and laminæ of the lower three lumbar, the sacral and the upper caudal vertebræ, and ends in fine tendons which are inserted into the transverse processes of the caudal vertebræ.

*Multifidus caudæ* is a continuation of the multifidus spinæ into the base of the tail, but it is soon replaced by short intervertebral muscles.

Of the short intervertebral muscles of the tail, three sets can be readily distinguished—fibres passing between the chevron bones, those linking up the transverse processes of adjacent vertebræ, *intertransversarii*, and *interspinales* attached to the dorsal aspect of the vertebræ.

*The Diaphragm* (text-fig. 41).—This muscle has the usual origin from

(*a*) The xiphoid cartilage, by two slips which are relatively large, being attached to the posterior surface and the lateral margins of the cartilage.

(*b*) The lower 6 costal cartilages.

(*c*) The arcuate ligaments which are not divisible into medial and lateral, but form on either side a uniform fibrous arch extending from the crus of the diaphragm to the last rib.

(*d*) *The Crura.* *The two crura are separated by the aorta,* which passes between them, lying well to the left of the *mid-line.* The right crus is much larger than the left and in its origin extends down to the upper end of the 3rd lumbar vertebra, whereas the left crus extends down to the middle of the 2nd. The right crus is split down the mid-line by a well-marked opening for the œsophagus, which reaches up to within 3 mm. of the central tendon.

The central tendon resembles closely the structure in *Tupaia.* It is trilobed, the central lobe being roughly square and large, and the lateral lobes small and attenuated. The perforation for the vena cava lies at the junction of the right lateral and central lobes as usual. The sympathetic chain passes beneath the arcuate ligament from the thorax into the abdominal cavity.

*Transversalis thoracis.*—This is a feeble muscle which takes origin from the deep aspect of the sternum and is inserted into the 3rd to 8th costal cartilages inclusive. The lower fasciculi are better developed than the rest of the muscle and run lateralwards from the last sternebra to the 8th costal cartilage.

*Psoas minor* is well developed. Above it is incompletely separated from psoas major, and so its precise origin is difficult to define. It rises mainly from the lower half of the lateral surface of the body of the last dorsal vertebra and the inter-vertebral disc below, and from the fascial covering of the psoas major. It is inserted by a strong flattened tendon 3 mm. broad into the pubic crest close to the symphysis.

*Psoas major.*—This muscle rises by fleshy fibres from the sides of the bodies and the bases of the transverse processes of the 2nd to the 5th lumbar vertebræ inclusive, as well as from the upper half of the body of the 1st sacral vertebra. It is inserted with iliacus into the lesser trochanter of the femur.

*Iliacus.*—This muscle, powerfully developed, consists of two separate parts, a lateral and medial. The medial rises, as usual, from the whole of the iliac fossa, and is about twice the size of the lateral or vertebral head. The latter takes origin by fleshy fibres from the transverse processes of all the lumbar vertebræ deep to the origin of the psoas major, and from the surface of quadratus lumborum lying deep. The muscle is separated from the psoas major by the femoral nerve and other branches of the lumbar plexus. The two parts of the iliacus muscle are readily separable from each other almost down to their insertion.

*Quadratus lumborum.*—This is also a strongly-developed muscle. It has a strong tendinous origin from the whole of the iliac crest, and these fibres gain insertion into the transverse processes of the lumbar vertebræ. Other fasciculi rise from the lumbar transverse processes, and are inserted into the lateral aspect of the bodies of the upper lumbar and lower thoracic vertebræ as high as the 9th thoracic.

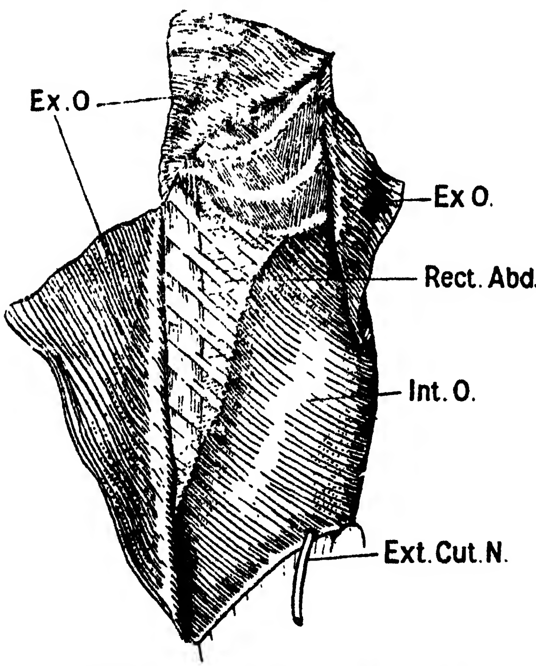
*The Intercostal muscles* are disposed in the usual manner, the external intercostals being replaced anteriorly at the lateral extremity of the sternal ribs by the anterior intercostal membrane.

*Subcostal muscles* are not present.

*The Abdominal Musculature.*

*M. Rectus Abdominis.*—This is a continuous narrow muscular band which is 65 mm. in length and averages about 5 mm. in breadth. It is attached below to the length of the pubic crest, and above is mainly inserted into the anterior half of the first

Text-figure 61.




Musculature of the Abdominal Wall. (× 1½.)

*Ex.O.* External oblique. *Rect.Abd.* Rectus abdominis. *Int.O.* Internal oblique. *Ext.Cut.N.* Lateral cutaneous nerve.

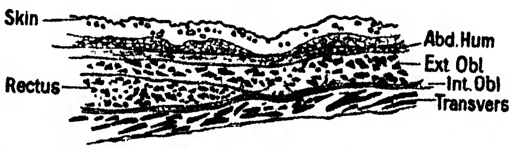
rib. A few fibres from its medial margin, however, gain attachment to the 2nd, 3rd, and 4th sternal ribs, and there is also a very slight attachment to the 8th, 9th, and 10th cartilages. On close scrutiny of the muscle with a dissecting microscope, the rudiments of two intersections were noted, one close to the xiphisternum, and one a little caudal to this.

*M. Pyramidalis* is apparently not differentiated, for this muscle could not be defined in any of the four specimens examined.

*M. Obliquus externus* is an extensive sheet of muscle rising by a series of digitations from the lower 10 ribs and very slightly from the lumbodorsal fascia. It appears to gain a feeble attachment to the ventral part of the iliac crest, and is mainly inserted into the inguinal ligament, to the anterior end of the symphysis pubis, and into the linea alba. The muscle continues fleshy right to the mid-line except at its cephalic extremity, where it forms a small patch of aponeurosis covering the rectus muscle. A minute inspection of the surface of the muscle showed what appeared to be traces of two tendinous intersections similar to those which are so well developed in *Tupaia ferruginea*. One of these is situated close to the subcostal margin and one midway between this and the inguinal ligament.

*M. Obliquus internus*.—Origin from the whole length of the inguinal ligament, the tip of the iliac crest, and the lumbodorsal fascia. It is inserted into the last three costal cartilages and by

Text-figure 62.




Transverse section passing through the lateral margin of the rectus sheath in the middle of the anterior half of the xiphipubic line to illustrate the disposition of the aponeurosis of the internal oblique in relation to the rectus abdominis. (× 15.)

an aponeurotic expansion into the linea alba. The junction of the muscular sheet and the aponeurosis forms an oblique line running from the subcostal margin caudally and medially to reach the mid-line a few millimetres above the symphysis pubis, as is shown in text-fig. 61. The transversalis thus appears to view behind the thin aponeurosis lateral to the rectus muscle in its cephalic half. The aponeurosis of the internal oblique at the lateral margin of the rectus is found to split into two laminæ, of which the posterior is thicker and passes posterior to the rectus, while the very attenuated anterior lamina passes to the linea alba in front of this muscle. This arrangement holds good down to the junction of the third and lower quarter of the abdominal course of the rectus, below which level the whole of the internal oblique and its aponeurosis passes anterior to the rectus. This disposition, found on dissection, was confirmed by the microscopical examination of transverse sections through the rectus sheath (text-fig. 62).

*M. Transversalis*.—This sheet takes origin from the last 6 ribs,

the lumbodorsal fascia, and the whole length of the inguinal ligament. The muscle remains fleshy practically to the mid-line, and is better developed anteriorly than posteriorly. The muscle passes behind the rectus except the caudal quarter of the muscle, which passes entirely in front, fusing with the internal oblique.

*The Cremaster* forms a relatively thick muscular sac lying in the scrotal cavity, and, as in *Tupaia*, is derived from both the internal oblique and the transversalis muscles.

## Summary and Discussion.

In the following pages, attention is drawn to points of interest which seem to bear upon the question of the position which *Ptilocercus* bears in relation to *Tupaia* and to other mammalia, especially the Lemuroidea. That this discussion is by no means exhaustive will be quite apparent. It will, however, serve the useful purpose of summarising briefly the anatomical data which have accumulated out of this investigation.

### External Characters.

The phalanger-like appearance of the general form of *Ptilocercus* which was noted by Gray (**11**) in his original description of the animal, receives an additional interest in view of the number of metatheroid features which its anatomy presents. The somewhat large size of the head and the well-developed eyes are to be noted. The ears stand in marked contrast to those of the genus *Tupaia*. Not only are they conspicuous in size, but they exhibit an interesting feature in the development of the antitragus into a flap-like process. This bears a very remarkable resemblance to similar formations found among the Cheiroptera. It may also be observed that an analogous process is formed in *Tarsius* from the plica principalis (**35**). The condition would appear to indicate considerable auditory acuity. The manus and pes can only be described as generalised, the palmar and plantar pads being arranged in the simplest and most primitive manner. The thenar and first interdigital pads of the foot, which in *Tupaia* are fused together, remain perfectly distinct in *Ptilocercus*. The extent of divergence of the hallux and pollex appears to be marked. Evidence of this is further derived from an examination of photographs of the living animal (Pl. I.) and from the features of the skeletal parts.

The arrangement of hairs on the tail in groups of three projecting from beneath each epidermal scale is extremely primitive. Such a condition is also found, though not with such diagrammatic simplicity, in the tails of some other mammals such as *Macroscelides*. There is no evidence that the tail of *Ptilocercus* is in any way prehensile.

The vibrissæ are well developed on the face, and the presence of carpal and calcaneal vibrissæ should be noted for comparison with the lipotyphlous insectivores.

## The Skeleton.

*The Skull.*—The significance of many of the features of the skull of *Tupaia* and *Ptilocercus* have already been discussed by Gregory (**13**). A general view of the skull of *Ptilocercus* shows it to be an evenly-proportioned structure with a moderately-developed brain-case, a tendency to reduction of the olfactory regions, and an absence of any conspicuous specialised modifications. The form of the mandible, the zygomatic and temporal regions indicate a relatively strong development of the masticatory muscles. The study of the skull may perhaps best be summarised by considering separately those features which are primitive or metatheroid and those which can be denoted as lemurine. At the same time, points of contrast with *Tupaia* may be noted.

1. *Primitive Features.*

(*a*) The premaxilla is relatively small, though it sends up a fine process which articulates with the frontal.

(*b*) The malar is extensive, reaching forward to come into contact with the lachrymal and back to the glenoid fossa. The backward extension may be regarded as metatheroid.

(*c*) The lachrymal extends on to the face, though not to a very marked degree. The lachrymal foramen is situated on the orbital margin.

(*d*) Exposure of the os petrosum on the base of the skull and of the mastoid on the lateral aspect.

(*e*) The tympanic bone preserves its simple annular form.

(*f*) The alisphenoid provides a well-marked tympanic wing which is hollowed out on its inferior aspect and forms a relatively large part of the roof of the tympanic cavity. This makes an interesting comparison with *Tupaia*, in which, although the bulla is relatively much larger and bulges further forward, the tympanic wing of the alisphenoid is much smaller.

(*g*) A small alisphenoid canal is present.

(*h*) The sphenoidal fissure and foramen rotundum are confluent.

(*i*) The cavity of the bulla is devoid of any but rudimentary septa.

(*j*) In its passage through the tympanic cavity the stapedial artery gives off a small ramus inferior.

(*k*) The basioccipital is short and wide.

(*l*) The palate is thinly ossified, but, unlike *Tupaia*, there are no palatal fenestræ. It is probable, however, that the fenestræ in *Tupaia* are to be regarded as secondary formations and not as primitive features.

2. *Lemurine Features.*

(*a*) The bony orbital margin is complete, a well-marked postorbital process of the frontal articulating with the frontal process of the malar.

(*b*) The malar is pierced by a foramen (sometimes double) for the passage of a branch of the zygomatic branch of the maxillary division of the 5th nerve.

(*c*) The plane of the orbital aperture is rotated forwards to an extent which brings it intermediate between that of *Tupaia* and that of *Lemur*. This, however, is undoubtedly correlated with the powerful development of the temporal muscle.

(*d*) There is no supraorbital foramen. Herein *Ptilocercus* contrasts with *Tupaia*. The absence of this foramen is clearly associated with the rotation of the orbital aperture mentioned above.

(*e*) The olfactory regions of the skull are generally reduced. The ectoturbinals are reduced to two as in *Lemur* and *Tupaia* (**27**) and in contrast with the Lipotyphla.

(*f*) The disposition of the cranial foramina (with the exception of the alisphenoid canal and the confluence of the sphenoidal fissure and the foramen rotundum) is similar to that found in Lemurs. In *Tupaia*, it may be noted, the sphenoidal fissure and the foramen rotundum are quite separate.

(*g*) The construction of the orbitotemporal region is essentially similar to the lemurine condition and differs from that of the lipotyphlous insectivora. In the latter the orbital surface of the maxilla is relatively large and has a wide articulation with the orbital plate of the frontal. The orbital plate of the palatine, which is very reduced in these forms, is thus excluded from contact with the lachrymal. In *Lemur* (**33**), *Ptilocercus*, and *Tupaia*, on the contrary, the orbital plate of the palatine is extensive, and reaches forward to the lachrymal, separating the frontal and maxilla, which nowhere articulate in the orbital cavity.

(*h*) The whole construction of the bulla from an entotympanic element, with the annulus tympanicus lying free inside, is identical with the lemurine condition, and is paralleled nowhere else among the Mammalia. In the course and arrangement of the arteries in the tympanic cavity, *Ptilocercus* also shows lemurine affinities. In view of the fact that the entocarotid is relatively large and a ramus inferior is given off by the arteria stapedia, *Ptilocercus* appears to be less closely related to the Lemuridæ than is *Tupaia*. In the latter the entocarotoid is markedly diminished and the ramus inferior is absent (**8**).

(*i*) The ossicula auditus bear close resemblances to those of *Lemur* and contrast strongly with those of the Lipotyphla.
(*j*) The posterior clinoid processes are conspicuously developed.
(*k*) There is an incipient partial flexion of the face on the basicranial axis.

*The Olfactory Cavity.*

The ethmoturbinal system is of a simple character, and corresponds to the type which has been described by Paulli (**27**) for the Insectivora and Lemuroidea. That is to say, there are four endoturbinals, including the nasoturbinal, and the second possesses two olfactory scrolls. The ectoturbinals are reduced to two, and here *Ptilocercus* agrees with *Tupaia* and contrasts with the Lipotyphla, in which the usual number is three. In the structure of Jacobson's organ, *Ptilocercus* corresponds closely to *Tupaia* (**3**). It shows affinity with marsupials, and differs strongly from the lipotyphlous insectivores in the shape of Jacobson's cartilage, in the presence of an outer bar of this cartilage, in the large size of the palatal papilla and the papillary cartilage, in the absence of a prolonged nasopalatine duct, etc. The presence of a posterior nasal floor cartilage is also to be regarded as a primitive feature.

*The Dentition.*

In this summary of the significant features of the dentition of *Ptilocercus*, I have made free use of the work of Gregory (**13**) (**17**), which I here acknowledge. The dental formula corresponds to that of *Tupaia*, and with the exception of the loss of the third upper incisor and the first premolars, is remarkably primitive. Compared with *Tupaia*, the upper incisors are enlarged. The second incisor has a posterior basal cusp, and its root is broad and is divided into anterior and posterior parts by a shallow vertical groove on its lateral aspect. The upper canine in *Ptilocercus* is double-rooted. The significance of this condition is perhaps not definitely decided, but there appears to be considerable evidence that a premolariform canine with two roots is to be regarded as a primitive mammalian feature. Osgood, on page 135 of his monograph on *Cœnolestes* (**24**), concludes: "On the whole, it appears that double-rooted, groove-rooted, or premolariform canines are found almost exclusively among forms exhibiting various primitive characters." The anterior two premolars are smaller in *Ptilocercus* than in *Tupaia*. The last upper premolar and the upper molars of *Ptilocercus* differ from those of *Tupaia* in having less pointed and lower cusps, in the absence of a mesostyle (which is bifid in *Tupaia*), in the better-developed hypocone, and in the presence of an internal cingulum. The procumbency of the lower incisors and the primitive

tritubercular pattern of the lower molars should be noted. Gregory notes that *Ptilocercus* shows a greater tendency to diprotodonty; that, in regard to the incisors, it approaches the primitive Zalambdodont *Microgale* more closely than does *Tupaia*; that in the greater reduction of the anterior two premolars it parallels the Shrews, *Myogale*, and other insectivores with enlarged anterior incisors; and that the molars indicate more omnivorous adaptations. He concludes as follows:—"In brief, the dentition of *Ptilocercus* has departed from the primitive Insectivore type, as represented in *Ictops*, in a tendency towards diprotodonty, reduction of the premolars, and omnivorous adaptation of the molars. The dentition of *Tupaia* has avoided these tendencies, but has emphasised the insectivorous features, such as enlarged styles, sharply-pointed cusps, etc., and a large and more or less divided mesostyle." He also concludes (**14**) that *Ptilocercus* is somewhat more lemur-like than *Tupaia* in its dentition.

*The Bones of the Forelimb*.—The well-developed clavicle shows no signs of a reduction. The scapula, as Gregory has noted (**14**), is broader than that of *Tupaia*. This author has also studied the humerus of *Ptilocercus* in relation to *Notharctus* (**17**). He remarks:—"The humerus of the existing *Ptilocercus* might readily be derived from the *Nothodectes* type by the lengthening of the shaft and slight reduction of the supinator crest. The *Ptilocercus* still retains much that is reminiscent of a *Nothodectes*-like type, but in *Tupaia* the crests are further reduced."

The conspicuous entepicondylar foramen and the prominent entepicondyle are probably primitive features, but the articular surfaces at the distal extremity of the humerus exhibit some interesting primate characters such as the distinct separation of the capitellum from the trochlea by the formation of a low external lip on the latter. The radius and ulna are completely separate, though there is a tendency for ossification to extend from the interosseous borders of these bones into the interosseous membrane. In this connection, Carlsson (**4**) records a specimen of *Tupaia javanica* in which the radius and ulna were bound together by a bony interosseous membrane. So far as can be ascertained from preserved specimens, the forearm of *Ptilocercus* is capable of a limited degree of supination.

The carpus contains a free os centrale such as is found in Lemurs but not in all Lipotyphla. The lunate shows a well-marked facet for articulation with the os magnum. Gregory (**13**) and Carlsson (**4**) note that the scaphoid and lunate are fused together in *Tupaia*. It is therefore interesting to note that in *Ptilocercus* these bones are completely separate, a condition which is at the same time more generalised and more lemurine. The form of the carpo-metacarpal joint of the pollex bears witness to the freedom of movement of which this digit is capable.

*The Bones of the Hindlimb.*—The ilium is more primitive than in *Tupaia* in its simple rod-like form, though a tendency to the spatulate form is shown in a slight hollowing-out of the lateral surface. The pectineal tubercle is of moderate size, and the pubic symphysis contrasts strongly with this joint in *Tupaia* in its shortness. It is instructive to note that Wood-Jones (**32**) some years ago anticipated a reduction of the symphysis in comparison with that of *Tupaia*, from a consideration of the more thoroughly arboreal mode of life of *Ptilocercus*. The femur has a straight shaft and a prominent lesser trochanter. The great trochanter does not project up quite as far as is the case in *Tupaia*. The patellar surface is relatively broad and shallow. The tibia and fibula are quite separate, the upper extremity of the latter showing an expansion which suggests the marsupial condition. Both malleoli are well developed. In the tarsus the astragalus is essentially similar to that of *Tupaia*, the remarkable resemblances of which to that of *Lemur* has already been discussed by previous authors. In *Ptilocercus* there is even a closer resemblance in that the astragalus does not articulate with the cuboid as it does in *Tupaia* (**4**). The entocuneiform is large, and shows an oblique saddle-shaped facet for the metatarsal of the hallux. There is no articulation between the mesocuneiform and the first metatarsal. The metatarsal and proximal phalanx of the hallux are stoutly built in comparison with the other metatarsals and phalanges, an indication of the independence of this digit.

## The Central Nervous System.

The features of the brain are such as might well be postulated for a primitive form of *Tupaia*, for, in most respects, the brain of *Ptilocercus* occupies a position which is intermediate between the brain of an Erinaceid type and that of *Tupaia minor* (**7**). Compared with the latter, the brain of *Ptilocercus* shows the following features:—The olfactory bulbs, olfactory tubercle, piriform lobe, and dentate gyrus are relatively larger. The optic nerves and tracts are smaller, the lateral geniculate body is less conspicuous and more simple in structure, the anterior colliculus is not so prominent, and the posterior colliculus is relatively larger. The medial geniculate body is well developed. Sections indicate, also, that in *Ptilocercus* the corpus callosum is more attenuated and the fornix system more predominant. The neopallium is distinctly more primitive. The frontal region is constricted, and the temporal lobe of the neopallial cortex is only faintly indicated by a slight curve downwards of the ectorhinal fissure. The only suggestion of a neopallial sulcus is the faint calcarine impression, and no incipient cortical foldings can be detected by microscopical study. In *Tupaia*, on the contrary, there is every indication of progressive cortical expansion. The frontal lobes in the brain of this animal are filled out, and the

temporal lobes are so well developed that only a narrow margin of the piriform lobe is visible from a lateral view. The in-rolling of the cortex on the dorsal surface of the corpus callosum is quite absent in *Ptilocercus*. The calcarine sulcus is distinct, and there are several sulci to be seen microscopically in the cortex of *Tupaia*. These microscopical sulci usually do not involve the surface of the cortex or contain a reduplication of pia mater, but there can be no doubt that they represent early stages in the formation of true cortical sulci. Similar appearances have been noted by Woollard in the brain of *Tarsius* (**36**).

Several of the features of the cortical lamination pattern are very instructive. It may be noticed, for instance, that in *Ptilocercus* the cingular areas occupy a broad band of cortex on the mesial surface of the cerebral hemisphere, stretching from the corpus callosum almost to the dorsomedial border, whereas, in *Tupaia*, they are constricted and partly buried from the surface by the expansion of neighbouring neopallial areas. It is in the details of the striate area, however, that there is to be found one of the most striking contrasts between *Ptilocercus* and *Tupaia*. In the latter the differentiation of this cortical type is remarkable, so that the extent of the area can be mapped out with great precision. I have elsewhere (7) described in some detail the unique distribution of this area in *Tupaia*, in which it extends downwards and forwards to the caudal extremity of the corpus callosum and is here even partly buried from the surface. In *Ptilocercus* the striate cortex is of a very simple type, shows very few distinctive features by which it can be differentiated from neighbouring areas, and occupies a much smaller extent of the occipital lobe.

The cerebellum is not quite so elaborated as in *Tupaia*.

On the whole, then, it may be said that, compared with *Tupaia*, the brain of *Ptilocercus* is more simple, shows a better development of the olfactory and the auditory regions, and a much more primitive condition of those parts of the brain associated with the sense of vision.

Also, relative to the body-weight, the weight of the brain as a whole is considerably less.

## The Cardiovascular System.

The characters of the heart call for no remark. It exhibits the generalised mammalian condition. The presence of a short brachiocephalic trunk on the left side corresponds to the usual condition found in *Tupaia*. There is some variation in this feature, however, for in one specimen of *Tupaia minor* I found the left common cartoid and subclavian arteries arising separately from the aortic arch. The absence of a common iliac artery may be regarded as a primitive feature. The significance of the details of the course of the vessels within the tympanic cavity are dealt with in connection with the skull.

The general arrangement of the arteries of the anterior extremity, in which the main artery in the brachium is represented by the art. brachialis superficialis, the brachial artery proper forming a relatively small vessel which accompanies the median nerve through the entepicondylar foramen, corresponds to the condition found in *Lemur catta* (Manners Smith). In the posterior extremity the arteria saphena is well developed. Manners Smith, in his monograph on "The Limb Arteries of Primates" (**22**). makes the statement that this vessel "lies on the m. sartorius in the lower mammals; in the higher the artery is covered by the muscle." It is interesting to note, therefore, that in *Ptilocercus* the artery is covered by the sartorius until it emerges from beneath the medial border of the muscle.

The termination of the external jugular vein, by forming a venous ring encircling the clavicle is worthy of remark, for this is clearly a condition which is capable of giving rise to either of the two common modes of ending of this vein, into the subclavian or into the axillary vein. The double precaval veins are to be found generally in animals of a primitive kind. The presence of a single vena azygos on the left side may have a different significance. Beddard, in his paper on "The Azygos Veins in the Mammalia" (**2**), notes that a single left azygos vein is found in many marsupials. He writes (p. 219): "Emphasizing the gap which separates the Marsupials from most of the higher mammals, it is noteworthy that in them (*i. e.* the Marsupials) it is the left azygos which is apt to be predominant, and not the right vessel." And again (p. 207): "My own observations confirm Dr. McClure when he remarks that a right azygos is characteristic of the genus *Macropus*, and that a left azygos is characteristic of the Phalangeridæ." This statement has especial interest in the present connection, when the metatheroid features to be found in the Tupaiidæ and the general phalanger-like appearance of the Pen-tailed Tree-Shrew are taken into account. The force of the implication, however, is somewhat diminished by Beddard's note that a left vena azygos is to be found in certain Rodents and Artiodactyles.

## The Digestive System.

*The Tongue.*—In the presence of a definite sublingua, *Ptilocercus* shows a resemblance both to the Marsupials and the Lemurs. This structure is, however, much more primitive in form than it is in *Tupaia*, as can be readily seen by reference to Carlsson's figures on p. 260 of her paper (**4**). In *Ptilocercus*, the sublingua is not so free and it has no lytta. The greater freedom and the presence of a sublingual lytta (which, however, contains no cartilage or muscular support) in *Tupaia* would appear to indicate a greater approximation to the lemurine condition. The lytta of the tongue is well developed, seemingly rather better so than in *Tupaia*. This condition is to be regarded as primitive,

and in the Lemurs the lytta exhibits a strong tendency to disappear. In *Tarsius* it is absent altogether. It is interesting to note that the tongue of *Ptilocercus* (and *Tupaia*) possesses all the essential characteristics which Sonntag (**28**) regarded as distinctive of the prosimian tongue. In addition, the accumulation of fungiform papillæ at the apex of the tongue of *Ptilocercus* bears witness to the development here of a special sensitivity such as Sonntag has already noted in the evolutionary development of the primate tongue. It should be remarked that Sonntag's statement is certainly incorrect that the frenal lamella is absent in *Tupaia* and that the lytta in the tongue of *Tupaia* is double.

The gastrointestinal tract is remarkable for its simplicity. The stomach is free from any elaboration, the duodenum, suspended by a mesentery, is pushed over to the right side and hidden from view by the irregular coils of the small intestine, and the whole of the pendent loop of the gut is formed from Meckel's tract attached to the posterior abdominal wall by the simplest form of dorsal mesentery. The colon forms a perfectly straight tube in which no differentiation can be detected except by reference to the vascular supply. The cæcum is similar in appearance to that found in all the Tupaiidæ except *Tupaia tana*, in which the cæcum is said to be absent. A review of Chalmers Mitchell's work on the intestinal tract of mammals (**23**) indicates that a condition of affairs comparable with that of *Ptilocercus* is only to be found among the Cheiroptera, and an exact parallel occurs in *Rhinopoma microphyllum*. Chalmers Mitchell compares the intestinal tract of this animal to that of birds, but he arrives at the conclusion that the simple gut pattern of bats has been secondarily derived from a more complex arrangement. He also states that so far "as evidence is afforded by the gut pattern, there is no reason to associate Cheiroptera with Insectivores." It follows, therefore, that a similar distinction, on the basis of the gut pattern, can be made between the Tupaiidæ and the Lipotyphla. It may be noted that there is no evidence that the simplicity of the intestinal tract of *Ptilocercus* is a secondary acquisition. On the contrary, it provides still further evidence of the remarkable primitiveness of the animal. In this connection, *Tupaia* shows a slight advance compared with *Ptilocercus*, for in that animal the proximal end of the colon is curved a little to the right, indicating the incipient appearance of a transverse colon. A further stage in the development of the colic tract is to be found in *Tarsius*, in which a transverse colon has been distinctly developed.

The Liver of *Ptilocercus* differs from that of *Tupaia* (**4**) in the following points :—

1. The relative sizes of the lobes. In *Tupaia* the left lobe is by far the largest, while in *Ptilocercus* the lobus centralis is the largest and the right lobe the smallest.

2. The position of the gall-bladder. In *Tupaia* this is situated at the right margin of the lobus centralis immediately adjacent to the right lobe. Carlsson points out that a resemblance is here shown to the condition found in the Prosimiæ, especially *Galago* and *Lemur*. In *Ptilocercus* the gall-bladder is situated in the middle of the right central lobule as is the case in the lipotyphlous Insectivora.
3. The presence of a fissura umbilicalis. This is absent in *Tupaia*, in which the two divisions of the central lobe are only indistinctly separated from each other.

In all these points it is probable that *Ptilocercus* is more generalised and primitive than *Tupaia*. The latter, on the other hand, shows in some ways a closer approximation to the lemurine condition. The anal glands may conveniently be referred to in this section. They are relatively well developed in *Ptilocercus*. Wood-Jones (**32**) notes similar glands in *Tupaia ferruginea*. They are present in *Tupaia minor*, but markedly diminished in size. This is undoubtedly correlated with the diminished importance of the olfactory sense in this animal.

### THE UROGENITAL SYSTEM.

In the male genitalia and the accessory sexual glands, *Ptilocercus* offers many points of contrast with *Tupaia*. In the former, the prostate is a compact glandular mass surrounding the urethra close to the neck of the bladder and opening by numerous ducts. The vas deferens shows a distinct ampulla and, before it reaches the urethra, it receives the duct of the vesicular diverticulum. The latter would appear to correspond to the seminal vesicle of human anatomy. In addition, there is a vesicular gland, similar in structure to the vesicular diverticulum of the vas, whose duct opens into the urethra close to but separately from the orifice of the common ejaculatory duct. Kaudern (**19**) has described in detail the male sexual organs of *Tupaia javanica*, and I have confirmed the accuracy of his description from a study of serial sections taken through the male urethra of one of my specimens of *Tupaia minor*. The homologies of the different glandular masses are not quite clear. A somewhat cursory examination would seem to indicate that what Kaudern describes as the prostate gland in *Tupaia*, a lobulated glandular mass opening on either side by a single main duct into the urethral canal some distance from the internal urinary meatus, really corresponds to what has been termed the vesicular gland in *Ptilocercus*. If this interpretation is correct, the prostate in *Tupaia* is represented only by a few trivial tubular glands embedded in the sphincter at the neck of the bladder. The question of these homologies is being studied in some detail in the laboratories at St. Bartholomew's Hospital by my friend Mr. Capener, and further discussion may therefore be

postponed till additional data are available. It is evident, however, that the condition in *Ptilocercus* is of a generalised nature, apparently capable of giving rise to the anthropoid or the lemuroid arrangement, while *Tupaia* shows a definite specialisation. Both *Tupaia* and *Ptilocercus* possess a well-developed uterus masculinus. The shape and proportions of the penis, and its position relative to the symphysis pubis, bear a remarkable resemblance to these features in Cheiroptera and many Primates, including man. In *Tupaia*, the proximal and distal parts of the urethra are relatively much more elongated and the glans penis is long and tapering. These characters are doubtless associated with the length of the symphysis pubis in this genus.

The testicle resembles closely that of *Tupaia* in its shape. Kaudern calls attention to the similarity between the cauda epididymis and the seminal reservoir of *Talpa* and Cheiroptera. A striking contrast lies in the fact that in *Ptilocercus* the testicles are not retained permanently in the scrotal cavity as is the case in *Tupaia*. In this connection, therefore, the former is more primitive and less lemur-like than *Tupaia*. Although in the latter the testicles are certainly permanently descended in the adult, I have always been able to demonstrate a patent but constricted channel leading from the saccus vaginalis into the peritoneal cavity. The parapenial position of the scrotal sac in *Ptilocercus* and *Tupaia* suggests an intermediate phase between the conditions to be found in the Metatheria and Eutheria.

## Myology.

The facial musculature is relatively well differentiated. This differentiation is perhaps further emphasised by the degree of complexity of the plexus formed by the facial nerve. The degree of development of the auricular musculature, which is in accordance with the development of the external ear, stands in contrast to the condition found in *Tupaia*, in which the pinna has a degenerate, hominoid appearance. The *sphincter colli* is less conspicuous than in *Tupaia*. The muscles of mastication show a powerful development, both the masseter and temporal muscles being readily subdivisible into component parts. In the neck region, the muscles exhibit a generalised disposition except that *scalenus anticus* is absent. Herein, *Ptilocercus* differs from *Tupaia* and approximates to the condition usually found in the lipotyphlous insectivores. In the presence of a well-developed *teres minor* and a *coracoid head of biceps*, however, the animal shows agreement with *Tupaia* and contrasts with the usual condition in the Lipotyphla. The complexity of *triceps* and the generalised form of *coracobrachialis* are also to be noted in this connection. The absence of a *brachioradialis* is a little puzzling. This muscle is normally developed in *T. minor* and *T. ferruginea* (6) as in Lemurs, and in lipotyphlous insectivores it is commonly absent. Either this muscle has disappeared in *Ptilocercus* or it

has not yet differentiated from the extensor carpi radialis mass which is prominently developed in this animal. In the latter case, its absence is to be regarded as a primitive feature. The independence of the *extensor longus pollicis* from the main mass of the *extensor profundus digitorum* appears to be an indication of the relative mobility of the pollex, but there is no independent long flexor for this digit. The *pronator teres* has no deep head, and so resembles the muscle as I have found it in specimens of *Tupaia* It may be noted that Wood-Jones (**34**) found a deep head in a specimen of *T. ferruginea*, but it would appear that this is not the usual arrangement. The *flexor sublimis* sends tendons to all four ulnar digits, that to the minimus being joined by a small tendon of a *flexor brevis manus*. It thus differs slightly from the arrangement in *Tupaia*, in which the whole of the tendon to the minimus is derived from the short flexor. *Pronator quadratus* is well developed. The small sesamoid bone developed in the common palmar tendon of *flexor profundus* apparently corresponds to the large bony plaque formed in the flexor tendons in the sole of the foot. In the palm, the *palmaris brevis* is well developed and the differentiation of the short flexors of the pollex and minimus digits are to be noted.

In the lower extremity, the following points call for remark. No distinct *tensor fasciæ femoris* could be found. I also failed to discover this muscle in *Tupaia*, though Leche (**21**) describes it in *T. ferruginea*. A strong *femorococcygeus* is present, and *gluteus medius* and *minimus* are well developed, the former being distinctly bilaminar. The presence of a distinct *piriformis*, which is also present in *Tupaia*, offers a contrast to the Lipotyphla in which this muscle is said to be absent. The conspicuous development of *caudofemoralis* in this connection must also be emphasised. On the other hand, *tenuissimus* is found generally in the Lipotyphla but is absent in the Lemurs. This latter muscle, however, representing as it does the femoral head of biceps in the higher Primates, is clearly a primitive feature. *Sartorius* is well developed, though it gains no direct attachment to the ilium. The *pectineus* and the full complement of the adductor muscles are present. On the extensor aspect of the thigh, the relative differentiation of the elements of the quadriceps mass should be noted, though no separate subcrureus was found. The origin of the *extensor longus digitorum* from the femoral condyle is probably a primitive arrangement. It is also found in *Tupaia*, but is not a lemurine condition. The differentiation of the peroneal group of muscles is, if anything, more marked than it is in *Tupaia*. The extent of the attachment of *popliteus* to the tibia agrees with that found in *Tupaia*, a feature which, as pointed out by Carlsson, is lemuroid. The formation of a tendon for the hallux from the *extensor brevis digitorum* and the differentiation of this part of the muscle to form a distinct *extensor brevis hallucis* is a feature of some considerable interest, for it appears that normally in the Lipotyphla such a tendon is

not developed. In *Ptilocercus* this condition is doubtless associated with a comparative freedom of movement of the hallux. The *flexor brevis digitorum* shows a remarkably generalised formation, each tendon having two well-defined heads of origin. The direct attachment of a large part of the origin of this muscle to the tuber calcis must also be emphasised. The abductors and short flexors of the hallux and minimus digits are all developed. Accessorius also forms a bulky muscle. The large plantar sesamoid developed in the long flexor tendons in the sole of the foot closely resembles that found in *Tupaia*. So far as I can ascertain, the only other mammals in which such a sesamoid is developed are the Dasypodidæ (**25**) and *Notoryctes* (**30**). A small sesamoid found in the tendons of origin of the short flexors in *Cænolestes* by Osgood (**24**) is probably not homologous with that of the Tupaiidæ.

In the hyoid region, the *digastric* muscle may be noted as differing from the condition found in *Tupaia*. In the latter, there is a well-developed central tendon connecting together the two bellies. In *Ptilocercus*, however, the two bellies are connected merely by a thin, oblique, tendinous intersection. This is probably a more primitive condition of the muscle. The omohyoid exhibits a well-marked oblique tendinous intersection between its anterior and posterior parts. The styloid muscles are all fully developed.

In the trunk, the psoas minor is conspicuous. The elements of the iliopsoas are fully differentiated, and the construction of the iliacus is similar to that found in *Tupaia*. Leche (**21**) has already pointed out the resemblance of the tupaioid arrangement to that of *Galago*.

The formation of the rectus sheath by the aponeuroses of the abdominal muscles substantiates the conclusions of Kaudern, who pointed out the lemurine condition to be found in *Tupaia* (**20**).

## General Conclusions.

Gregory, as a result of a comparative study of the dentition and the skeleton, concluded that, on the whole, *Ptilocercus* is more lemur-like than *Tupaia* in the characters of its skull and dentition, but that, in regard to the post-cranial skeleton, it is distinctly less lemurine. He therefore makes the perfectly legitimate suggestion that many of the lemurine features to be found in *Tupaia* are secondarily associated with arboreal habits of life, and thus indicate no real affinity to the Prosimiæ. A complete survey of the anatomy of these animals, however, leads to conclusions that are somewhat different. In every part of its anatomy, *Ptilocercus* shows some remarkable contrasts with *Tupaia*. The brain of *Ptilocercus* is much more primitive and macrosmatic in type. The visual regions of the brain are poorly developed compared with *Tupaia*, while the auditory centres are distinctly better developed. With this difference is associated

a corresponding difference in the development of the peripheral sense-organs. It appears that *Ptilocercus*, which has evidently adopted nocturnal habits, shows a tendency to specialise in the direction of auditory acuity and has retained a primitive brain in which the olfactory regions have undergone relatively little reduction. *Tupaia*, on the other hand, which is a diurnal animal, exhibits to a remarkable degree a progressive development of all those anatomical structures which are concerned in the reception of visual stimuli and a corresponding diminution of the olfactory apparatus of the brain. In other words, the activities of this animal are related much more closely to visual impressions and are less dependent upon the influence of olfactory stimuli. Such a condition, the predominant influence of the visual sense, is precisely what Elliot Smith has held to be one of the fundamental characteristics of the Primate phylum as contrasted with other mammalian groups. It is therefore of additional interest to note that in many other ways *Tupaia* shows a greater affinity with the Lemuroidea than does *Ptilocercus*, e. g., in a greater elaboration of the neopallium as a whole, in certain features of the postcranial skeleton, in the differentiation of certain muscles, in many characters of the male genital system and especially the permanent descent of the testes, in the features of the liver, in certain details of the vessels in the tympanic cavity, in the tongue, in the diminution of the anal scent-glands, etc. *Tupaia*, however, shows some definite specialisations of a generic type, *e.g.*, in the carpus and tarsus, the teeth, and some of the genital glands, and in relation to these, *Ptilocercus* is at the same time more primitive and more lemurine. These points are, however, relatively few. Broadly speaking, it may be said that *Ptilocercus* and *Tupaia* represent two successive phases in the evolutionary development of a lemurid from a primitive, insectivorous, eutherian mammal. *Ptilocercus* is a remarkably generalised and primitive arboreal mammal. *Tupaia* exhibits many differences from *Ptilocercus*, and these differences in almost every case indicate a closer approach to the Lemuroidea. Such conclusions serve to emphasise the truth of the supposition that there is a very real affinity between the Tupaiidæ and the Lemuridæ.

## Acknowledgements.

However much one may desire to do so, it is virtually impossible to render full acknowledgements to all sources from which assistance has been derived in the preparation of a monograph such as this. In addition to references and acknowledgements already made, however, I feel that it is due to me here to express my obligations a little more explicitly towards certain workers in the field of anatomy. To Professor Elliot Smith I owe a great deal. It was his illuminating work on the evolutionary origin of the Primates with special reference to the brain which stimulated

me to investigate more thoroughly than had hitherto been done the morphology of the Tupaiidæ, and which urged me to search every possible means of obtaining specimens of *Tupaia* and the exceptionally rare *Ptilocercus* in a sufficiently good state of preservation to enable a detailed study of their anatomy to be made. He has been kind enough, also, to allow me from time to time to discuss with him the work which I was doing and to make many useful suggestions to me.

From the published work of Dr. Gregory of New York, I, like many other comparative anatomists, have derived help to an extent which it is difficult to estimate. His studies on the classification of the Mammalia and his magnificent monograph on *Notharctos* are standard works of reference of which I have made free use.

To my friend, Dr. Woollard, I am indebted for many advantages the expression of which in words is not possible. I may say here that in his paper on *Tarsius*, Dr. Woollard has set a high standard in monographic studies, and it has been my endeavour in the present paper to maintain this standard.

For technical assistance, I wish to express my gratitude to Mr. T. J. Poulton, who gave me much useful advice in the preparation of the text-figures, to Mr. F. W. Bond of the London Zoological Society, for his photographs of the teeth and limb bones, and to Miss Vaughan of the Dunn Laboratory, St. Bartholomew's Hospital, for the microphotographs reproduced on Plate V.

## EXPLANATION OF THE PLATES.

### Plate I.

Photographs of the living *Ptilocercus*. (Photos by Mr. Jee Koo, Sarawak Museum.)

### Plate II.

A. Limb bones of *Ptilocercus*. × 2. 1. Right Os Innominatum. 2. Left Scapula. 3. Left Clavicle. 4. Left Femur. 5. Left Humerus. 6. Left Tibia. 7. Left Fibula (which has been figured upside down). 8. Left Ulna. 9. Left Radius. 10. Left Tarsus, viewed from the dorsal aspect after removal of the astragalus. 11. Left Astragalus viewed from the dorsal aspect. (Photo by F. W. Bond.)

B. Radiograph of the Pes and Manus of *Ptilocercus*.

### Plate III.

A. Upper and Lower Teeth of *Ptilocercus*. × 4 (about).

B. Upper and Lower Teeth of *Ptilocercus*, with exposure of the roots. × 2 (about). (Photos by F. W. Bond.)

### Plate IV.

Skeleton of *Ptilocercus* (prepared at the British Museum). Natural size. (Photo by Martin C. Hinton, Esq.)

PLATE V.

Microphotographs of sections through the cortical areas of the cerebrum. × 60. A. Area Gigantopyramidalis. B. Area Striata. C. Area Frontalis. D. Area Parietalis. E. Area Temporalis. The figures refer to Brodmann's laminæ. (Photos by Miss Vaughan.)

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# EXHIBITIONS AND NOTICES.

## October 19th, 1926.

Sir A. Smith Woodward, F.R.S., Vice-President, in the Chair.

The Secretary read the following Report on the Additions to the Society's Menagerie during the months of June, July, August, and September, 1926:—

### June.

The registered additions to the Society's Menagerie during the month of June were 206 in number. Of these 61 were acquired by presentation, 2 were deposited, 122 were purchased, 6 were received in exchange, and 15 were born in the Menagerie.

The following may be specially mentioned:—

A young Californian Sea-Lion (*Otaria californiana*), born in the Menagerie on June 13th.

A Tasmanian Devil (*Sarcophilus harrisi*), purchased on June 17th.

A Blacksmith Plover (*Hoplopterus speciosus*), a Bronze-winged Courser (*Rhinoptilus chalcopterus*), and two Pied Babblers (*Crateropus bicolor*), from South Africa, new to the Collection, purchased on June 3rd.

A Three-banded Plover (*Oxyechus tricollaris*), from South Africa. presented by Messrs. A. W. Gamage on June 3rd.

### July.

The registered additions to the Society's Menagerie during the month of July were 247 in number. Of these 141 were acquired by presentation, 17 were deposited, 68 were purchased, 10 were received in exchange, and 11 were born in the Menagerie.

The following may be specially mentioned:—

2 young male Giraffes (*Giraffa camelopardalis camelopardalis*), a male and female Sudanese Oryx (*Oryx algazel*), 3 Shoebills (*Balæniceps rex*), from the Sudan, purchased from the Sudan Government on July 1st.

A male Chimpanzee (*Anthropopithecus troglodytes*), from the Gold Coast, presented by Arthur Haserick, F.Z.S., on July 25th.

A Vociferous Sea-Eagle (*Haliaëtus vocifer*), from South Africa, presented by Major Albert Pam, F.Z.S., on July 21st.

A Coach-Whip Bird (*Psephodes crepitans*), from Australia, presented by Capt. H. S. Stokes, M.C., F.Z.S., on July 27th.

A collection of Imperial Scorpions (*Pardimus imperator*), from Gambia, presented by H.E. Capt. Sir Cecil H. Armitage, K.B.E., C.M.G., D.S.O., F.Z.S., on July 19th.

A collection of Land-Crabs (*Cardisoma armata*), from Gambia, presented by H.E. Capt. Sir Cecil H. Armitage, K.B.E., C.M.G., D.S.O., F.Z.S., on July 19th.

A Violaceous Plantain-eater (*Musophaga violacea*), from Gambia, presented by H.E. Capt. Sir Cecil H. Armitage, K.B.E., C.M.G., D.S.O., F.Z.S., on July 28th.

A large collection of Fishes and other Marine specimens, obtained from the coast of Madeira by E. G. Boulenger, Esq., F.Z.S.

## August.

The registered additions to the Society's Menagerie during the month of August were 157 in number. Of these 83 were acquired by presentation, 7 were deposited, 27 were purchased, 1 was received in exchange, and 39 were born in the Menagerie.

The following may be specially mentioned:—

A young Hippopotamus (*Hippopotamus amphibius*), born in the Gardens on August 20th. (The last example reared in the Gardens was born on November 5th, 1872.)

1 Lion Cub (*Felis leo*), from Kenya Colony, presented by Major C. S. Ramsay-Hill, M.C., F.Z.S., on August 14th.

2 Thick-tailed Opossums (*Didelphys crassicaudata*), purchased on August 13th.

1 Noble Macaw (*Ara nobilis*), presented by C. H. West on August 10th.

7 Versicolor Teal (*Querquedula versicolor*), purchased on August 13th.

2 Brush-Turkeys (*Catheturus lathami*), hatched in the Gardens on August 21st.

## September.

The registered additions to the Society's Menagerie during the month of September were 240 in number. Of these 180 were acquired by presentation, 1 was deposited, 25 were purchased, 1 was received in exchange, and 33 were born in the Menagerie.

The following may be specially mentioned:—

A Nagor Antelope (*Cervicapra redunca*), bred in the Menagerie on September 1st.

A collection of animals, from Gambia, presented by H.E. Capt. Sir Cecil H. Armitage, K.B.E., C.M.G., D.S.O., F.Z.S., on September 2nd.

An Aard Vark (*Orycteropus æthiopicus*), from Abyssinia, purchased on September 7th.

A young Musk-Ox (*Ovibos moschatus*) and a Polar Bear (*Thalarctos maritimus*), from East Greenland, presented by the Cambridge East Greenland Expedition on September 11th.

A Red Brocket (*Mazama rufa*), an Ocelot (*Felis pardalis*), and a Great Anteater (*Myrmecophaga tridactyla*), from South America, presented by Mr. Alexander Muir on September 15th.

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Dr. P. A. Buxton, F.Z.S., exhibited, and made remarks upon, apparatus for the Measurement of Radiant Heat in the Tropics.

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Major E. E. Austen, D.S.O., F.Z.S., exhibited, and made remarks upon, specimens of *Chrysomyia chloropyga*, Wied, a Fly from Salisbury, South Rhodesia, and drew attention to what he considered to be an Ancestral habit.

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## November 2nd, 1926.

Prof. E. W. MacBride, F.R.S., Vice President, in the Chair.

Col. S. Monckton Copeman, M.D., F.R.S., F.Z.S., exhibited, and made remarks upon, a nest and eggs of the Black-chinned Humming-Bird (*Archilochus alexandri*), which he had received from Dr. W. H. Mills of San Bernardino, California, through the courtesy of Dr. W. C. Hanna. The nest had been built on a Willow-twig, four feet from the ground. Col. Monckton Copeman also drew attention to two specimens of *Calypte anna* (♂ and ♀), and a third (young ♂), received from Mr. Donald R. Dickey of Pasandina, Californa, and from Mr. Allen Brooks of Okanagan Landing, British Columbia. The species shown are the only ones, of seven native to California, which are known to have hybridized. Dr. Mills has determined, from continuous personal observation, that in the case of *Calypte anna*, the period of incubation is fourteen days: and that in about an equal period subsequently the young will have left the nest.

## November 16th, 1926.

Sir Sidney F. Harmer, K.B.E., F.R.S., Vice-President in the Chair.

The Secretary read the following Report on the Additions to the Society's Menagerie during the month of October, 1926:—

The registered additions to the Society's Menagerie during the month of October were 156 in number. Of these 73 were presented, 5 were purchased, 5 were received in exchange, and 73 were born in the Menagerie.

The following may be specially mentioned:—

1 Puma (*Felis concolor*), 1 Pinche Marmoset (*Œdipomidas œdipus*), from Colombia, and 2 Peba Armadillos (*Tatusia novæ-*

*cincta*), from Venezuela, presented by Lady Richmond Brown, F.Z.S., on October 4th.

3 Large Anacondas (*Eunectes murinus*), from Venezuela, presented by F. A. Mitchell-Hedges, F.Z.S., on October 4th.

1 Javan Chevrotain (white var.) (*Tragulus javanicus*), from Malay, presented by W. L. S. Besapa, on October 8th.

1 Brown Tree-Kangaroo (*Dendrolagus inustus*), from N.W. New Guinea; 2 De Brun's Wallabies (*Macropus brunii*), 1 Greater Bird-of-Paradise (*Paradisea apoda*), and 1 King Bird-of-Paradise (*Cicinnurus regius*), from the Aru Islands; 1 Wallace's Bird-of-Paradise (*Semioptera wallacei*), new to the Collection, from Batchian Island; 2 Yellow-throated Hanging Parrakeets (*Loriculus pusillus*), new to the Collection, from Java, and 4 Three-coloured Parrot-Finches (*Erythrura trichroa*), from New Guinea, presented by J. Spedan Lewis, Esq., F.Z.S., on October 25th.

Dr. G. D. Hale Carpenter, F.Z.S., exhibited, and made remarks upon, a series of lantern-slides illustrating the bionomics of the Tsetse Fly, *Glossina palpalis*, in connection with Sleeping Sickness, and drew especial attention to the food and breeding-places, and the effect of climate on the length of life of the fly.

**['Proceedings,' 1926, Part III. (pp. 683–940), was published on September 15th, 1926.]**

# INDEX OF ILLUSTRATIONS.

# INDEX.

## 1926.—Pages 683–1314.

[New names in clarendon type. Systematic references in italics (Z.S.L.) indicates additions to the Society's Menagerie.]

PRINTED BY TAYLOR AND FRANCIS, RED LION COURT, FLEET STREET.

No. 277.

# ABSTRACT OF THE PROCEEDINGS

OF THE

# ZOOLOGICAL SOCIETY OF LONDON.*

**June 1st, 1926.**

Sir JOHN BLAND SUTTON, Bt., F.R.C.S., Vice-President, in the Chair.

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THE SECRETARY read a Report on the Additions to the Society's Menagerie during the month of April, 1926.

Dr. FRANK CHAPMAN exhibited, and made remarks upon, a series of Lantern slides illustrating the Bird and Mammalian Life on the Barro Colorado Island, Panama.

Mr. A. S. LE SOUËF, C.M.Z.S., gave an account of some of his observations on "The Habits of the Order Marsupialia."

Prof. R. T. LEIPER, M.D., F.R.S., F.Z.S., gave an account, illustrated by Lantern-slides, of the two following communications:—(1) "The Starling as a Factor in the Spread of Gapeworm Disease in Chickens"; and (2) "Some Parasites of Rats in the Zoological Society's Gardens."

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* This Abstract is published by the Society at its offices, Zoological Gardens, Regent's Park, N.W., on the Tuesday following the date of Meeting to which it refers. It will be issued, along with the 'Proceedings,' free of extra charge, to all Fellows who subscribe to the Publications; but it may be obtained on the day of publication at the price of *Sixpence*, or, if desired, sent post-free for the sum of *Six Shillings* per annum, payable in advance.

Mr. S. ZUCKERMAN, M.A., gave a *résumé* of his paper on "Growth Changes in the Skull of the Baboon (*Papio porcarius*)."

In the absence of the Authors, the following papers were taken as read :—STANLEY HIRST, F.Z.S., "Descriptions of new Mites, including Four new Species of Red Spider"; J. H. POWER, F.Z.S., "Note on the Occurrence of Hybrid Anura at Lobatsi, Bechuanaland Protectorate"; H. C. WILKIE, F.R.C.V.S., F.R.M.S., F.Z.S., "The Ossicula auditus of the Common Badger (*Meles taxus*)."

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The next Meeting of the Society for Scientific Business will be held on Tuesday, June 15th, 1926, at 5.30 P.M., when the following communications will be made :—

H. HAROLD SCOTT, M.D., F.R.C.P., D.P.H., F.Z.S.

A Mycotic Disease of Batrachians.

HAROLD G. JACKSON, F.Z.S.

The Morphology of the Isopod Head.

F. W. EDWARDS.

On the Marine Chironomidæ (Diptera); with Descriptions of a new Genus and Four new Species from Samoa.

P. A. BUXTON, F.Z.S.

The Colonisation of the Sea by the Chironomidæ (Diptera); with an Account of the Habits of a new Genus and Species in Samoa.

OMERA A. MERRITT HAWKES, M.Sc.

On the Massing of the Ladybird, *Hippodamia convergens* (Coleoptera), in the Yosemite Valley.

Marie V. Lebour, D.Sc., F.Z.S.

On some Larval Euphausiides (Crustacea) from the Mediterranean in the Neighbourhood of Alexandria, Egypt, collected by Mr. F. S. Russell.

D. Bhatia, M.Sc., F.R.M.S.

On Three new Species of the Genus *Anadenus* (Mollusca).

Prof. J. P. Hill, F.R.S., F.Z.S., and Prof. J. Bronte Gatenby, D.Sc., Ph.D.

The Corpus Luteum of the Monotremata.

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The following Papers have been received:—

Prof. D. M. Fedotov.

The Plan of Structure and Systematic Status of *Ophiocista* (Echinodermata).

J. R. Norman, F.Z.S.

A Synopsis of the Rays of the Family Rhinobatidæ, with a Revision of the Genus *Rhinobatus*.

Dr James Waterston, F.Z.S.

On the Crop Contents of certain Mallophaga (Insecta).

Dr. R. Anthony, C.M.Z.S., and G. M. Iliesco.

Etude sur les Cavités nasales des Carnassiers.

Malcolm A. Smith, M.R.C.S., L.R.C.P., F.Z.S.

The Function of the "Funnel" Mouth of the Tadpoles of *Megalophrys*, with a Note on *M. aceras* Boulenger.

---

The Publication Committee desire to call the attention of those who propose to offer Papers to the Society, to the great increase in the cost of paper and printing. Papers should be condensed and be limited so far as possible to the description of new results.

Communications intended for the Scientific Meetings should be addressed to

P. CHALMERS MITCHELL,
*Secretary.*

ZOOLOGICAL SOCIETY OF LONDON,
REGENT'S PARK, LONDON, N.W. 8.
*June 8th*, 1926.

No. 278.

# ABSTRACT OF THE PROCEEDINGS

OF THE

# ZOOLOGICAL SOCIETY OF LONDON.*

**June 15th, 1926.**

Prof. E. W. MacBride, F.R.S., Vice-President,
in the Chair.

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The Secretary read a Report on the Additions to the Society's Menagerie during the month of May, 1926.

The Secretary communicated some notes on a young female Chimpanzee presented to the Society by T. D. Maxwell, Esq.

Major S. S. Flower, O.B.E., F.Z.S., exhibited, and made remarks upon, models of a White Elephant from Siam.

Dr. H. H. Scott, F.R.C.P., D.P.H., F.Z.S., gave a *résumé* of his paper "A Mycotic Disease of Batrachians."

Dr. R. J. Tillyard, F.R.S., C.M.Z.S., gave an account of "Some new Orders of Fossil Insects," illustrated by a remarkable series of lantern-slides.

Professor Henry Fairfield Osborn, C.M.Z.S., President of the American Museum of Natural History, who was present, said that he would like to felicitate Dr. Tillyard upon his recent

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researches, and at the same time to cong ... upon the progress it had made since his last visit to London some fifteen years ago.

Mr. HAROLD J. JACKSON, F.Z.S., communicated his paper on "The Morphology of the Isopod Head."

Dr. P. A. BUXTON, F.Z.S., gave a *résumé* of his paper on "The Colonisation of the Sea by the Chironomidæ (Diptera)," and of a paper by Mr. F. W. EDWARDS on "The Marine Chironomidæ (Diptera); with an Account of the Habits of a new Genus and Four new Species from Samoa."

Mrs. ONERA A. MERRITT HAWKES, M.Sc., communicated her paper "On the Massing of the Ladybird, *Hippodamia convergens* (Coleoptera), in the Yosemite Valley."

In the absence of the Authors, the following papers were taken as read:—MARIE V. LEBOUR, D.Sc., F.Z.S., "On some Larval Euphausiides (Crustacea) from the Mediterranean in the Neighbourhood of Alexandria, Egypt, collected by Mr. F. S. Russell"; D. BHATIA, M.Sc., F.R.M.S., "On Three new Species of the Genus *Anadenus* (Mollusca)"; Prof. J. P. HILL, F.R.S., F.Z.S., and Prof. J. BRONTE GATENBY, D.Sc., Ph.D., "The Corpus Luteum of the Monotremata."

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The next Meeting of the Society for Scientific Business will be held on Tuesday, October 19th, 1926, at 5.30 P.M.

A notice stating the Agenda for the Meeting will be circulated early in October.

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The following Papers have been received:—

**Prof. D. M. FEDOTOV.**

**The Plan of Structure and Systematic Status of *Ophiocista* (Echinodermata).**

J. R. Norman, F.Z.S.

A Synopsis of the Rays of the Family Rhinobatidæ, with Revision of the Genus *Rhinobatus*.

Dr. James Waterson, F.Z.S.

On the Crop Contents of certain Mallophaga (Insecta).

Dr. R. Anthony, C.M.Z.S., and G. M. Iliesco.

Étude sur les Cavités nasales des Carnassiers.

Malcolm A. Smith, M.R.C.S., L.R.C.P., F.Z.S.

The Function of the "Funnel" Mouth of the Tadpoles of *Megalophrys*, with a Note on *M. aceras* Boulenger.

G. H. Lockett, B.A., and W. S. Bristowe, B.A.

Observations on the Mating Habits of some Web-spinning Spiders.

Prof. Julian Huxley, F.Z.S.

Studies in Heterogonic Growth: the Annual Increment of the Antlers of the Red Deer (*Cervus elaphus*).

R. I. Pocock, F R.S., F.Z.S.

(1) The External Characters of the Patagonian Weasel (*Lyncodon patagonicus*).

(2) The External Characters of *Thylacinus sarcophilus* and some related Marsupials.

O. W. Richards, B.A., and G. C. Robson, M.A., F.Z.S.

The Land and Freshwater Mollusca of the Scilly Isles and West Cornwall.

A Collection of Papers by the following Authors, dealing with the Results of the Cambridge Expedition to the Suez Canal, 1924:—H. Munro Fox; E. Heron-Allen and A. Earland; M. Burton; Prof. A. Billard; E. T. Browne; Dr. Th. Mortensen; Dr. Hj. Broch; R. Gurney; M. H. Leigh-Sharpe; Prof. W. M. Tattersall; J. Omer-Cooper; Dr. W. T. Calman; Dr. A. Balss; C. D. Soar; C. H. N. Jackson; J. R. le B. Tomlin; G. C. Robson; Miss A. B. Hastings; S. T. Burfield; V. C. Robinson; H. Harant; and J. R. Norman.

The Publication Committee desire to call the attention of those who propose to offer Papers to the Society, to the great increase in the cost of paper and printing. Papers should be condensed and be limited so far as possible to the description of new results.

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Communications intended for the Scientific Meetings should be addressed to

P. CHALMERS MITCHELL,

*Secretary*

ZOOLOGICAL SOCIETY OF LONDON,

REGENT'S PARK, LONDON, N.W. 8.

*June* 22*nd*, 1926.

No. 279.

# ABSTRACT OF THE PROCEEDINGS

OF THE

# ZOOLOGICAL SOCIETY OF LONDON.*

October 19th, 1926.

Sir A. SMITH WOODWARD, F.R.S., Vice-President, in the Chair.

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THE SECRETARY read a Report on the Additions made to the Society's Menagerie during the months of June, July, August, and September, 1926.

Dr. P. A. BUXTON, F.Z.S., exhibited, and made remarks upon, apparatus for the Measurement of Radiant Heat in the Tropics.

Major E. E. AUSTEN, D.S.O., F.Z.S., exhibited, and made remarks upon, specimens of *Chrysomyia chloropyga*, Wied, a Fly from Salisbury, South Rhodesia, and drew attention to what he considered to be an Ancestral habit.

Miss JOAN B. PROCTER, F.L.S., F.Z.S., exhibited, and made remarks upon, a white example of the English Grass-Snake.

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Prof. JULIAN HUXLEY, F.Z.S., gave a *résumé* of his paper, "Studies in Heterogonic Growth: the Annual Increment of the Antlers of the Red Deer (*Cervus elaphus*)."

Dr. JAMES WATERSTON, F.Z S., communicated his paper "On the Crop Contents of certain Mallophaga (Insecta)."

Dr. F. A. BATHER, F.R.S., F.Z.S., communicated a paper by Prof. D. M. FEDOTOV on "The Plan of Structure and Systematic Status of *Ophiocista* (Echinodermata)."

In the absence of the Authors, the following papers were taken as read:—J. R. NORMAN, F.Z.S., "A Synopsis of the Rays of the Family Rhinobatidæ, with a Revision of the Genus *Rhinobatus*; Dr. R. ANTHONY, F.Z.S., and G. M. ILIESCO, "Étude sur les Cavités Nasales des Carnassiers."

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The next Meeting of the Society for Scientific Business will be held on Tuesday, November 2nd, 1926, at **5.30** P.M., when the following Communications will be made:—

Col. S. MONCKTON COPEMAN, M.D., F.R S., F Z.S.

Exhibition of Photographs of the Nest and Eggs of a Californian Humming-Bird.

Dr. G. M. VEVERS, F.Z.S.

Report on a Hippopotamus recently born in the Society's Gardens.

HUGH B. COTT, B.A., F.Z.S.

Observations on the Life-Habits of some Batrachians and Reptiles from the Lower Amazon; and a Note on some Mammals from Marajó Island.

W. E. LE GROS CLARK, F.R.C.S., F.Z.S.

On the Anatomy of the Pen-tailed Tree-Shrew (*Ptilocercus lowii*).

O. W. Richards, B.A., and G. C. Robson, M.A., F.Z.S.

The Land and Freshwater Mollusca of the Scilly Isles and West Cornwall.

Malcolm A. Smith, M.R.C.S., L.R.C.P., F.Z.S.

The Function of the "Funnel" Mouth of the Tadpoles of *Megalophrys*, with a Note on *M. aceras* Boulenger.

---

The following Papers have been received:—

R. I. Pocock, F.R.S., F.Z.S.

(1) The External Characters of the Patagonian Weasel (*Lyncodon patagonicus*).

(2) The External Characters of *Thylacinus*, *Sarcophilus* and some related Marsupials.

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G. H. Locket, B.A., and W. S. Bristowe, B.A.

Observations on the Mating Habits of some Web-spinning Spiders.

Edith M. Sheppard, M.Sc., F.Z.S.

Revision of the Family Phreatoicidæ (Crustacea) with a Description of Two new Species.

Chi Ping.

On the Structures of the Hard Palate of *Felis tigris*.

H. H. Woollard, M.D.

The Differentiation of the Retina in the Primates.

Oldfield Thomas, F.R.S., F.Z.S.

The Delacour Exploration of French Indo-China.—Mammals.

---

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Communications intended for the Scientific Meetings should be addressed to

P. CHALMERS MITCHELL,
*Secretary, Zool. Soc.*

ZOOLOGICAL SOCIETY OF LONDON,
REGENT'S PARK, LONDON, N.W. 8.
*October* 26*th*, 1926.

No. 280.

# ABSTRACT OF THE PROCEEDINGS

OF THE

# ZOOLOGICAL SOCIETY OF LONDON.*

**November 2nd, 1926.**

Prof. E. W. MacBride, F.R.S., Vice-President, in the Chair.

Col. S. Monckton Copeman, M.D., F.R.S., F.Z.S., exhibited, and made remarks upon, a nest and eggs of the Black-chinned Humming-Bird (*Archilochus alexandri*), which he had received from Dr. W. H. Mills of San Bernardino, California, through the courtesy of Dr. W. C. Hanna. The nest had been built on a Willow-twig, four feet from the ground. Col. Monckton Copeman also drew attention to two specimens of *Calypte anna* (♂ and ♀), and a third (young ♂), received from Mr. Donald R. Dickey of Pasandina, Californa, and from Mr. Allen Brooks of Okanagan Landing, British Columbia. The species shown are the only ones, of seven native to California, which are known to have hybridized. Dr. Mills has determined, from continuous personal observation, that in the case of *Calypte anna*, the period of incubation is fourteen days: and that in about an equal period subsequently the young will have left the nest.

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Dr. G. M. Vevers, F.Z.S., communicated a report on a Hippotamus (*H. amphibius*) recently born in the Society's Gardens.

Mr. Hugh B. Cott, B.A., F.Z.S., give a *résumé* of his "Observations on the Life-Habits of some Batrachians and Reptiles from the Lower Amazon; and a Note on some Mammals from Marajó Island.

Dr. W. E. Le Gros Clark, F.R.C.S., F.Z.S., communicated his paper on "The Anatomy of the Pen-tailed Tree-Shrew (*Ptilocercus lowii*)."

Dr. Malcolm A. Smith, M.R.C.S., L.R.C.P., F.Z.S., communicated his paper on "The Function of the 'Funnel' Mouth of the Tadpoles of *Megalophrys*, with a Note on *M. aceras* Boulenger."

Mr. G. C. Robson, M.A., F.Z.S., gave a *résumé* of his paper with Mr. O. W. Richards, B.A., on "The Land and Freshwater Mollusca of the Scilly Isles and West Cornwall."

---

The next Meeting of the Society for Scientific Business will be held on Tuesday, November 16th, at 5.30 P.M., when the following Communications will be made:—

Dr. G. D. Hale Carpenter, F.Z.S.

The Biology of *Glossina palpalis* in connection with Sleeping Sickness.

R. I. Pocock, F.R.S., F.Z.S.

(1) The External Characters of the Patagonian Weasel (*Lyncodon patagonicus*).

(2) The External Characters of *Thylacinus*, *Sarcophilus* and some related Marsupials.

H. Munro Fox, M.A.

General Report on the Cambridge Expedition to the Suez Canal, 1924.

G. H. Lockett, B.A., and W. S. Bristowe, B.A.

Observations on the Mating Habits of some Web-spinning Spiders.

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H. H. Woollard, M.D.

The Differentiation of the Retina in the Primates.

Oldfield Thomas, F.R.S., F.Z.S.

The Delacour Exploration of French Indo-China.—Mammals.

Robert Gurney, M.A., F.Z.S.

Some Australian Fresh-water Entomostraca reared from Dried Mud.

Major S. S. Flower, O.B.E., F.L.S., F.Z.S.

Loss of Memory accompanying Metamorphosis in Amphibians.

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Communications intended for the Scientific Meetings should be addressed to

P. CHALMERS MITCHELL,
*Secretary, Zool. Soc.*

ZOOLOGICAL SOCIETY OF LONDON,
REGENT'S PARK, LONDON, N.W. 8.
*November 9th*, 1926.

No. 281.

# ABSTRACT OF THE PROCEEDINGS

OF THE

# ZOOLOGICAL SOCIETY OF LONDON.*

**November 16th, 1926.**

Sir SIDNEY F. HARMER, K.B.E., F.R.S., Vice-President, in the Chair.

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The SECRETARY read a Report on the Additions made to the Society's Menagerie during the month of October, 1926.

Dr. G. D. HALE CARPENTER, F.Z.S., exhibited, and made remarks upon, a series of lantern-slides illustrating the bionomics of *Glossina palpalis* in connection with Sleeping Sickness, and drew especial attention to the food and breeding-places, and the effect of climate on the length of life of the fly.

Mr. R. I. POCOCK, F.R.S., F.Z.S., gave a *résumé* of his papers on (1) "The External Characters of the Patagonian Weasel (*Lyncodon patagonicus*)," and (2) "The External Characters of *Thylacinus*, *Sarcophilus*, and some related Marsupials."

Mr. H. MUNRO FOX, M.A., communicated his "General Report on the Cambridge Expedition to the Suez Canal, 1924."

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